2027

THE JOURNAL

OF

ANIMAL BEHAVIOR

VOLUME 3, 1913

CONTENTS OF VOLUME 3, 1913

NUMBER 1, JANUARY-FEBRUARY

NUMBER 2, MARCH-APRIL

NUMBER 3, MAY-JUNE

NUMBER 4, JULY-AUGUST

CONTENTS

Subject and Author Index
VOLUME 3

Original contributions are marked by an asterisk (*)

A STUDY OF THE RESPONSES OF RODENTS TO MONOCHROMATIC LIGHT

JOHN B. WATSON AND MARY I. WATSON

The Johns Hopkins University

The following study on the responses of rodents to monochromatic light was begun in January, 1911 and was completed in May, 1912. Experiments were discontinued in the summer of 1911. From every standpoint the experiments are far from being satisfactory. It is believed, however, it may be said at the outset, that this paper offers some clear evidence that a differential response on the basis of wave length is not possible in the case of the rat. The tests (in Experiment II) upon the rabbits were never completed. The results of what tests we gave them are so similar to those obtained from the rats that we believe that the total outcome of the work on the rabbits would have been essentially the same as that reported for the rats.

The experiments were made with the color apparatus essentially as it is described in Yerkes and Watson's monograph [1] and by the two color discrimination method there suggested. The discrimination method is in such general use that no description of it is necessary.

EXPERIMENT I

January 11, 1911–June 15, 1911.

The two stimulus lights were *red* ($\lambda = 6550$) and *green* ($\lambda = 5050$). In this first experiment the two bands were not equated in energy. They were projected directly upon the plaster surface as they came from the selecting slit. Only two animals were worked with—a pure white rat and a grey Belgian hare. Both were about half grown at the beginning of the experi-

---

[1] Yerkes and Watson. *The Behavior Monographs.* 1911, vol. 1, no. 2.

ment. *Red* was the positive color. Food was given with *red*
but denied with *green*. No punishment was introduced. The
animals were fed for several days in the food box before the
stimulus lights were admitted.

Training experiments upon the rat and the rabbit began
January 27th. Nineteen days from the beginning of training
the animals reached a high percentage of accuracy and there-
after never made more than one or two errors in a normal series.
The number of trials per day was 15. Experiments were made
daily without interruption for 39 days.

TABLE I
Showing Rise of Red-green Habit

Days	Rat, % correct	Rabbit, % correct
1	50	73
2	53	33
3	53	46
4	66	46
5	73	60
6	73	53
7	73	53
8	80	80
9	60	86
10	53	93
11	73	75
12	73	86
13	73	91
14	53	76
15	66	93
16	53	93
17	86	80
18	66	93
19	86	93
20	86	93
21	86	93
22	93	100
23	93	100
24	100	80
25	93	86
26	93	100
27	93	93
28	100	93
29	100	100
30	93	93
31	93	93
32	93	100
33	100	100
34	100	93
35	86	100
36	86	100
37	100	100
38	93	100
39	100	100

Considered ready for control series.   Considered ready for control series.
   Total number of trials, 555.   Total number of trials, 555.

While there is nothing wonderful in the formation of this discrimination habit, it does become significant when we contrast it with our failure to get such a habit set up with the *yellow* and *blue* (see page 7). If modern color theories have any phylogenetic reference at all we would expect the formation of the *red-green* habit to be much slower than that of the *yellow-blue*. Taken at their face value the records invite three possibilities of interpretation:—

1st, the animals are discriminating upon the basis of difference in wave length;

2nd, upon the difference in intensity between the two lights;

3rd, only one stimulus is effective (for whatever reason) and no real discrimination is involved. It is possible that the *red* chosen lies outside the spectrum of one or both animals. On this hypothesis the habit might be formed easily. Yerkes,[1] Washburn,[2] Hess,[3] and Watson,[4] have all remarked upon the apparent low stimulating power of *red* light. Another fact which must be taken into consideration in connection with the two stimuli discrimination method, which may have some bearing upon the present work, is the one discussed by Dr. Clara Jean Weidensall. Her results were reported at the Washington meeting of the American Psychological Association (December, 1911). In her work on the discrimination of two *grays* differing greatly in intensity it was shown that, usually, only one stimulus is effective. In other words it is possible to get apparent discrimination between two stimuli where no real discrimination is involved. A further discussion of this point will be given upon page 6.

These three possibilities of interpretation were not clearly foreseen in the early stages of the experiments. Two things lead us to a favorable consideration of the view that the *red* lay outside the animals' spectrum. (1) The fact that, in the control experiments (to be cited below), the complete elimination of *red* failed to change the responses of the animals, and

---

[1] Yerkes, Robert M. The Dancing Mouse, New York, 1907.
[2] Washburn, M. F. and Abbott, E. Experiments on the Brightness Value of Red for the Light Adapted Eye of the Rabbit. *Jour. Animal Behavior.* 1912, vol. 2, pp. 145-180.
[3] Hess, C. Experimentelle Untersuchungen zur vergleichenden Physiologie des Gesichtssinnes. *Arch. f. d. ges. Physiol.* 1911, Bd. 142, S. 405-446.
[4] Watson, J. B. Some Experiments Bearing Upon Color Vision in Monkeys. *Jour. Comp. Neurol. and Psychol.* 1909, 1, vol. 19, pp. 1-28.

(2), as will appear in Experiment II, the failure to get discrimination at all between *yellow* and *blue* under similar circumstances. In other words if both colors used in Experiment I had possessed stimulating value, no habit would have been formed under the conditions there obtaining.

Since at the completion of the above set of tests we had no suspicion that the *red* was not stimulating the animals, we began control experiments which were designed to show whether the animals were responding to the difference in wave length or to the difference in intensity. We had planned a rather wide series of tests. We had intended to leave the *red* at full intensity and then gradually to lessen the intensity of the *green* with the rotating sector, and then to repeat the procedure, allowing *green* to remain at the standard intensity. It was hoped either to establish the fact that the habit would maintain itself regardless of the intensity factor, or that at some point where the intensities were equal for the animal, the habit would break down. A few preliminary tests were taken with such astonishing results that we had completely to re-envisage the problem. We cite a few of the experiments:—

1911.

March 7th. *Red* full intensity. *Green* cut to 11% of full intensity. 15 trials. 93% correct.

March 8th. *Green* full intensity. *Red* cut to 11% of full intensity. 15 trials. 100% correct.

March 9th. *Red* full intensity. *Green* cut to 2.7% of full intensity. 11 trials. 40% correct. Complete loss of discrimination. Then immediately afterwards 9 trials were given with both stimuli at full intensity. 100% of correct choices.

March 10th. Conditions as beginning of test on previous day. 15 trials. 53% correct. Complete loss of discrimination. 5 trials were then given with both stimuli at full intensity. 100% correct.

March 11th. Normal series. 15 trials. 100% correct.

From March 11th to May 16th certain experiments were tried to determine the effect of external illumination upon the discrimination. These experiments were so unsatisfactory that mention of the results is omitted. By June 5th the animals were again trained to discriminate perfectly between *red* and

green. Further control experiments to determine the nature of the effective stimulus were then undertaken.

June 5th. Eight normal trials were first given. 100% correct. Then *red* beam was cut out; *green* left at full intensity. Went to *red side* (darkness) on every trial (10 trials).

June 6th. Eight normal trials. 100% correct. Then *green* was cut out and *red* left at full intensity. *Right position habit developed immediately.* Discrimination lost. Then 4 normal trials were given. 100% correct.

June 7th. Eight normal trials. 100% correct. *Green* out, *red* at full intensity. 14 trials given. *Right position habit developed immediately.* 4 normal trials were then given. 100% correct.

June 10th. Eight normal trials given. 100% correct. *Red* cut out; *green* full intensity. Went to *red side* (darkness) on all 15 trials. 2 normal trials were next given. Both correct.

June 11th. Six normal trials given. 100% correct. *Green* out; *red* full intensity. *Left position habit developed immediately.* (9 trials.) Then 10 normal trials were given. 90% correct.

June 12th. Six normal trials given. 100% correct. *Both* lights cut out for 15 trials. *Right position habit developed.* 4 normal trials were given. 100% correct.[5]

The detailed experiments upon the rabbit are not given. They are identical in character and number with those given the rat. The results are exactly the same except that in the case of the rabbit a decrease of 50% in intensity of the *green* produced disturbance. The work of Washburn and Abbott on the rabbit, showing the lack of stimulation by *red*, had not appeared when our work was completed. Our results are in complete harmony with respect to *red*.

These results seem to show perfectly that the green was the effective stimulus and that the *red* had no stimulating value whatsoever. *The animals were avoiding a lighted compartment.* One might decrease the intensity of the *green* light enormously and eliminate the *red* altogether without changing the accuracy of the responses. When, however, the intensity of the *green*

---

[5] In all of the control experiments food might be had regardless of stimulus light reacted to. Food was always kept in both compartments even during the training series.

approaches the threshold, as on March 9th, a disturbance imme-
diately manifests itself. Whenever the *green* was cut out the
animal behaved exactly as though no light stimulus was present
(contrast tests on June 11th with those on June 12th). These
results seem to show that we are dealing here with a defect in
the receptor rather than with the lack of "attention" cited in
Dr. Weidensall's report.

Summarizing the results of Experiment I we find:

1st, that the *green* was the effective stimulus;

2nd, that the *red* had no stimulating effect,—it probably was
not discriminated from total darkness. The results harmonize
with the hypothesis that the *red* chosen lay outside of the
animal's spectrum. Decisive experiments upon this point now
in progress, but carried out under different conditions, will soon
be reported upon.

It is clear that Experiment I does not touch the problem of
sensitivity to differences in the wave lengths which lie within
the animal's spectrum.

EXPERIMENT II

On account of the fact that in Experiment I only one stim-
ulus was effective, which made it impossible to test the problem
of differential sensitivity with *red* and *green*, we began in the
fall of 1911 to test another group of rodents with *yellow*
(λ=5950) and *blue* (λ=4780). The stimulus lights were not
equated in energy during the training series but were projected
directly upon the plaster surfaces. To the human eye the *yel-
low* was enormously more intense. Before control experiments
began the *yellow* and *blue* were equated in energy. The energy
value chosen is given by Pfund in the Yerkes and Watson Mono-
graph, p. 81.

January 9th. We began taking records upon two gray Bel-
gian hares and three rats,—one black and white and two pure
white. All of the animals had just reached the age of sexual
maturity. We were unfortunate in the case of our rabbits.
Not one completed the experiment. All three of the rats con-
tinued work throughout the experiment. Experiments upon all
five of the animals were begun on January 9th. The training
series is given for only four of the animals. The record of only
one rabbit is given. We had hoped to carry through all of the

tests upon Polly, a rabbit which Professor Washburn kindly gave us; one used in her recent light work. Polly had been used to working in illumination and nothing would induce her to work steadily in darkness. All of the other animals worked perfectly under the conditions of the experiment. The animal which is trained while young to work in a dark room goes about the task in a perfectly normal manner.[6]

The marks of the animals are given as follows:

Rat   I.   Pure white rat, male: fed with *blue*.
Rat   II.   Pure white rat, male: fed with *yellow*.
Rat III.   Hooded black and white rat, male: fed with *blue*.
Rabbit.   Gray Belgian Hare, male: fed with *blue*.

It will be seen that the records are not inter-comparative. The two white rats were working with different positive colors. Rat III, although fed with the same color as Rat I, was a black and white rat and consequently possessed pigmented eyes. These differences are especially noted in order that too great uniformity in records may not be demanded.

Table II shows the records made by each animal. We began with two stimuli, then on the 22nd day changed to one stimulus. On the 38th day we changed back to two stimuli. Punishment was introduced in each case on the day designated.

A careful consideration of these records shows, we think, that the discrimination between *yellow* and *blue* was not perfected during the time limits of the experiment. Had we desired to prolong the work the habit would probably have been formed. The paper of Hoge and Stocking (this Journal, vol. II, p. 43) shows that a habit of responding to one of two white lights, 2 and 16 cp. respectively, can be formed by the rat in about 500-600 trials. Had the difference in intensity been less, a much larger number of trials would probably have been necessary. On the assumption that the animals used in the present experiment were reacting to a difference in intensity, we would expect the habit to be formed after a sufficient number of trials. Unfortunately there are no intensity experiments on the Weber-Fechner law in the cases of rats and rabbits to guide us. Since more than 500 trials were given we assume that the relative

---

[6] Indeed our experience during the past two years at Hopkins has given us complete confidence in the dark room work. Any argument advanced concerning the "unnaturalness of the conditions" should be supported by experimental proof before receiving consideration.

JOHN B. WATSON AND MARY I. WATSON

TABLE II

Showing Lack of Discrimination When Both Stimuli Are Presented at Full Intensity

Date	Rat I (*Blue*) % correct	Rat II (*Yellow*) % correct	Rat III (*Blue*) % correct	Rabbit (*Blue*) % correct
1	60 (2)	60 (2)	70 (2)	60 (2)
2	60	60	20	50
3	40	70	80	70
4	50	40	60	60
5	50	60	70	60
6	50	60	70	70
7	40	10	90	60
8	50	—	10	50
9	40	10	30	50
10	50	20	40	50
11	60	50	60	60
12	70	—	40	60
13	70	60	20	90
14	60	40	70	50
15	60	50	90	80
16	70	70	30	80
17	30	80	80	50
18	40	30	40	60
19	50	40	50	60
20	57	20	40	60
21	57	20	50	60
22	50 (1)	40 (1)	50 (1)	80 (1)
23	80	60	73	70
24	90	70	90	80
25	60	60	60	90
26	90	60	90	70
27	70	50	100	90
28	60	60	80	80
29	80	30	80	90
30	30	50	100	50
31	90	70	100	70
32	100	70	80	70
33	60	60	90	90
34	100	30 (P)	100	60 (P)
35	80	40	90	80
36	100	10	—	—
37	80	60	100	90
38	80 (2)	60 (2)	90 (2)	80
39	70 (P)	70	30 (P)	80
40	50	80	40	80
41	50	70	80	90
42	70	60	50	100
43	70	60	35	100 (2)
44	70	60	80	90
45	70	80	60	80
46	50	70	80	60
47	60	70	40	60
48	10	100	40	80
49	20	90	40	60

(1) One stimulus introduced.
(2) Second stimulus introduced.
(P) Punishment introduced.
(−) No record for that day.

intensity difference between the *yellow* and *blue* for the animals was less than that between the 2 cp. light and 16 cp. light used in the Hoge and Stocking work. This would account for the failure of our animals to form the habit on the assumption of brightness difference.

Our reason for not prolonging the tests was that we wished to try the method of training the animals to respond to one stimulus (the positive or food stimulus) and then gradually to introduce the second (the light reacted against). Table III shows the results.

TABLE III

SHOWING RAPID RISE OF HABIT WHEN ONE STIMULUS (POSITIVE) IS PRESENTED[7]

Days	Rat I (*Blue*) % correct	Rat II (*Yellow*) % correct	Rat III (*Blue*) % correct	Rabbit (*Blue*) % correct
1	100	30	80	90
2	80	40	80	100
3	70	80	90	90
4	60	70	100	80
5	50	80	70	70
6	60	90	100	90
7	60	80	90	90
8	100	70	100	80
9	60	60	100	100
10	90	100	100	100
11	100	100	100	100
12	90	100	100	70
13	80	60	90	80
14	100	100	70	80
15	90	100	60	90
16	90	70	90	80
17	100	100	100	80
18	100	100	100	100
19	90	100	100	80
20	100	100	100	90
21	100	100	100	100
22	100	100	100	100
23	100	100	100	80
24	100	100	100	100
25	100	100	100	80
26	60	90	100	100
27	100	90	100	90
28	100	100	100	90 ·
29	100	100	100	·90
30	100	90	100	100
31	70	100	100	90
32	100	90	100	100
33	100	100	100	70

[7] It will be remembered that all of these animals had previously worked with one stimulus for about 200 trials (see table II).

All the animals being sufficiently automatic in their responses to one stimulus, we decided gradually to *introduce* the second stimulus. Accordingly both lights were equated in energy. Then the light reacted against was cut down by means of the rotating sector. Table IV shows the results.

In the case of Rat I and the Rabbit (reacting positively to *blue*) the introduction of the second stimulus at the energy designated produced no break down in the habit. The association was maintained fairly well up to the point of equal energy. Rat III (black and white, reacting positively to *blue*) shows extreme unsteadiness for a time after the energy of the *yellow* had been increased to one-tenth that of the blue. This may be due to the fact that the *yellow* possesses slightly more stimulating value for him than for the white rats and the rabbit. Consequently the introduction of the *yellow* (although graduated to the same energy values as for the other animals) was for him more abrupt than for them. The records show that after one or two break downs this animal became very steady. The failure of Rat II to discriminate shows, we think, even without further control tests, that *yellow* has very low stimulating value. Since he was habituated to respond to an intensity value which for him did not lie very high in the scale he was disturbed by the *blue* the moment its intensity equaled that of *yellow*. This point is reached when the energy of the *blue* is one-eighteenth that of *yellow*. All of our tests are in harmony with the view that *blue* has a tremendously high stimulating value.

After Rats I and II had learned to discriminate between the lights at equal energies, control tests were introduced for the purpose of finding out whether the discrimination could be held, whatever the energy relations between the two stimuli. On account of the approach of summer, when the tests were to be discontinued we did not gradually cut down intensity of light *reacted against* as we had previously planned. Instead we chose a variety of tests which we thought would show most rapidly whether the animals were responding to wave length difference or to intensity difference. We give an individual diary record of tests on Rat I. The results of tests on Rat III are quite similar to those reported for Rat I.

TABLE IV

SHOWING EFFECT ON HABIT OF LEAVING POSITIVE COLOR AT FULL INTENSITY
AND GRADUALLY INTRODUCING COLOR REACTED AGAINST

Rat I
(Reacting positively to *blue*)

Days	Angular opening on *yellow*	% correct
1	10	90
2	10	83
3	10	93
4	20	93
5	30	100
6	40	93
7	50	100
8	60	93
9	70	90
10	80	95
11	90	100
12	100	100
13	110	85
14	110	100
15	120	100
16	130	93
17	140	93
18	180	93
19	200	93
20	200	100
21	240	93
22	360 (*)	96
23	360 (*)	100

This shows almost perfect discrimination at equal energy.

Rat III
(Reacting positively to *blue*)

Days	Angular opening on *yellow*	% correct
1	10	100
2	20	86
3	20	86
4	20	100
5	30	85
6	30	33
7	— (1)	80
8	30	40
9	— (1)	100
10	10	75
11	10	60
12	10	95
13	20	100
14	30	75
15	30	85
16	30	95
17	40	93
18	50	100
19	60	100
20	80	80
21	80	83
22	80	85
23	100	100
24	140	100
25	360 (*)	96

Perfect discrimination at full intensity.

Rat II
(Reacting positively to *yellow*)

Days	Angular opening on *blue*	% correct
1	10	80
2	10	80
3	10	80
4	10	90
5	20	80
6	20	75
7	20	90
8	30	80
9	30	77
10	30	50
11	30	60
12	— (1)	94
13	10	100
14	20	80
15	20	75
16	20	80
17	20	60
18		
19		
21		

18, 19, 21. Could not be brought to full intensity. Shows that animal was reacting to brightness and that *blue* at 20-30° was as bright as the *yellow* at full intensity.

Rabbit
(Reacting positively to *blue*)

Days	Angular opening on *blue*	% correct
1	10	70
2	10	83
3	10	100
4	20	80
5	20	90
6	30	93
7	40	80
8	40	90
9	50	90
10	60	85
11	60	95
12	70	95
13	80	90
14	90	93
15	100	94
16	110	85
17	110	93
18	120	93
19	140	85
20	140	93
21	150	86
22	180	90
23	220	85
24	220	93
25	360 (*)	80

Animal died. Was discriminating fairly well at equal energy. Death was due to cancerous growth upon neck; during the past month growth had increased enormously in size. Animal worked faithfully until the day before his death.

(1) Only one stimulus used for that day.
(*) Equal energy.

Control tests on Rat I (reacting positively to *blue*)

May 3rd. After normal series at equal energies [8] *blue* was cut to 20° opening. Animal set up *right position* habit. Discrimination lost. Normal series (5 trials) given again. Animal went to *blue* as usual. The behavior of Rat II (*yellow*) had prepared us for this type of result. The *blue* to them is high in the scale of intensity; the *yellow* very low. When the *blue* was brought down to one-eighteenth the energy of the *yellow*, the two stimuli were too nearly equal in intensity to afford a basis for a differential response. It may be argued that we had reduced the intensity of the *blue* below the animal's threshold. A long series of experiments shows that the *blue* still stimulates the animals when the angular opening is between 1 and 2 degrees. The *yellow* threshold, on the other hand, lies much higher. Our reason for not reporting upon this is due to the fact that we have made the threshold tests throughout the spectrum a separate study. It may be safely taken for granted that the threshold for *blue* is below a 5° opening, whereas that for *yellow* is probably not much below 10° [9] (lower, somewhat, for the black and white rat than for the white).

May 4th. Normal series of 10 trials, all correct, *blue* cut out. Animal was frightened at first (the change in condition for him must have been large) and would hardly respond at all. First trial went to *blue* side (darkness); then went to *yellow* (light side) on every trial for 9 trials. Equal energy series of 5 trials then given. Went to *blue* on every trial.

May 5th. Normal series, equal energies, 10 trials, 100% correct. Then *blue* was cut to 10°, *yellow* full intensity. 7 trials. Animal fell back on position habit. Went to right on every trial. Then *blue* was cut out for 10 trials. Went to *yellow* on every trial. Next *blue* was cut to 10°. 6 trials. Went to *yellow* on every trial.

May 6th. *Yellow* full intensity, *blue* cut to 10°. 10 trials given. Went to *yellow* on every trial.

The test upon these two days with 10° opening upon *blue*

[8] By normal series, we mean in all cases about ten trials with both stimuli at equal energy (unless otherwise stated).

[9] In most places in this paper the angular opening is given. This is for the convenience of anyone desiring to repeat the work. If the relation in terms of energy is desired, it will be remembered that the work of Brodhun and of Hyde abundantly proves the Talbot-Plateau law.

show that we are working with the stimuli at the point where they possess approximately equal stimulating power. We get one of two reactions without being able to predict which will occur, *viz.*, a break down in habit or a complete reversal with respect to choice of light. Possibly our inability to predict the response may be due to slight fluctuations in the current supplying the arc, which would alter the intensity of the two lights unequally (the distribution of energy in the spectrum of any source varies greatly, depending upon the temperature at which the source is burned).

Similar tests upon Rat II (reacting positively to *yellow*)

Table IV shows that this animal never learned to discriminate between the *yellow* and *blue* at anything like equal energies. This gave us an opportunity to test the question of reversal in choice of positive light. The tests show without discussion that his discrimination had been based upon the difference in intensity.

April 26th. Gave series of 15 trials with *yellow* as only stimulus, 93% correct. This was done to bring animal back to normal habit of reacting to one stimulus. Then for 7 trials full intensity *blue* was substituted for the *yellow*. *Went to blue on every trial.*

April 27th. *Yellow* and *blue* full intensity, 10 trials. *Chose blue on every test.* Then *blue* was cut out and *yellow* given alone. 10 trials, 80% correct.

April 30th. *Yellow* alone, full intensity, 15 trials, 100% correct.

May 1st. *Yellow* and *blue* full intensity, 20 trials. *Went to blue on every trial.* This shows the same results as tests on April 27th.

Another series of tests was undertaken where *white* light (from Nernst filament projected direct upon plaster surface) was substituted for *blue* or *yellow* at will.[10]

May 16th. *Yellow* (animal's positive color) at full intensity. Nernst in place of *blue*. 9 trials. Animal went to *white* light on every trial. Immediately following this test one was given in which *white* light was substituted for *yellow*. 10 trials. Went to *white* light on every trial.

May 17th. Another series was given with identical results.

[10] It will be remembered that Washburn suggested this type of test at the Boston meeting of the American Psychological Association (1910).

CONCLUSIONS

1. The evidence seems to justify the conclusion that the long wave lengths stimulate the visual receptors of the rodents very slightly or not at all. Where their spectrum begins at the red end cannot be decided by the above type of experimentation.

2. Experiment II offers good but not absolutely conclusive evidence that the rats can respond only to difference in intensity of monochromatic light. On account of the low stimulating value of *red* and *yellow* our choice of stimuli was not very good. *Blue* and *green* would have been better. To the adherents of color theories the denial of a response based upon wave length, both in the case of *red* and *green* and of *yellow* and *blue* is the equivalent of denying the possibility of a response on the basis of wave length anywhere in the animal's spectrum. If the data on *blue* and *green* were at hand and spoke as clearly for intensity difference, we believe that we could say with some certainty that wave length is not a factor in the visual responses of rodents.

A PRACTICAL DEVICE TO SIMULATE THE WORKING OF NERVOUS DISCHARGES

S. BENT RUSSELL

St. Louis, Missouri

First we shall briefly outline a theory which will reconcile observed facts as to the structure of nervous systems and the reactions of such systems. We will then take up the description of a practical mechanical contrivance which will represent the essential elements of a nervous system and which will react in the same way. We will then compare the results obtained with the machine with those given by live nervous connections. In this discussion we shall confine our field to the interactions of the nerves. What happens in sensory endings like those of smell and taste does not concern us. The reader should also avoid thinking of what he knows of his own sensations and have in mind only what he can observe in the nervous systems of other creatures.

A nervous system may be taken as controlling several pairs of opposing muscles through a system of nervous channels excited by a number of sensory terminals. A muscular movement or response is caused by a combination of discharges from several channels acting on a given muscle or muscles more than on the muscle or muscles directly opposed to it or them. The said combination of discharges may be excited at one or several sensory points.

As a result of individual experience changes take place in the nervous channels. With the same sensations [1] as before we observe that the responses have changed and vice versa we observe the same responses when the sensations have changed. The most natural explanation for this is that some of the channels have grown more than others, that is, that they have become more open to the flux.

The problem that is before us is to account for the growth

---

[1] Throughout this article the term *sensation* is used to represent the excitement of a sensory terminal of a nervous channel. Of course this departure from the usual subjective meaning of the word is made for the sake of brevity.

of certain channels more than others. Take the familiar but perplexing case of inhibition of muscular action shown here by diagram. (Figure 001.) Let S_1 and S_2 be sensations. M_1 represents a forward movement, M_2 a backward movement. S_1, M_1 and S_2, M_2 are channels of good conductivity. The cross channel S_1, x, M_2 is of low conductivity so that before experience is gotten, sensation S_1 gives response M_1 a forward movement. After experience is had we observe the sensation S_1 is followed by response M_2, a backward movement. We conclude that channel S_1, x, M_2 has as a result of experience become of high conductivity, exceeding S_1, M_1. How can we explain this? How can experience have developed the weak channel and not the strong one?
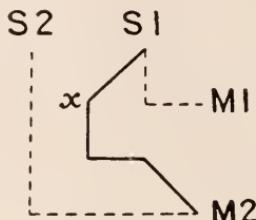
FIGURE 001

Now, as to the conductivity of nerves we find evidence to support the following premises:

1. The effect at the motor end of a nervous channel is not always in proportion to the intensity of the impression at the sensory end. We may state it thus: The susceptibility of a nervous channel is greater at one time than at another or conversely we may state: The resistance of a channel to nervous discharges is less at one time than at another. The same rule will hold it is believed even though the nerves forming the channel considered be perfectly normal as to nourishment; that is to say that normally nourished nerves are of variable susceptibility.

2. The first discharge through a channel after a period of rest will increase the susceptibility. If the impression at the sensory end is repeated at proper short intervals the susceptibility will be steadily increased.[2]

[2] Spencer, Herbert. Principles of Psychology. New York, 1894, pp. 577, 614. Thorndike, E. L. Animal Intelligence. New York, 1911, p. 267.

3. If the impressions are followed by a period of rest, the longer the rest the greater will be the decrease found in the susceptibility. That is to say the susceptibility of a channel decreases with disuse.[3]

4. There is, however, a permanent increase in the susceptibility of a nervous channel caused by repeated discharges.

5. If a given channel has several sensory endings S_1, S_2, S_3 and one or more motor endings M, a discharge from S_1 to M will increase the susceptibility to a discharge from S_2 or S_3 to M. Hence if S_1 and S_2 are excited in succession there will be a temporary increase in the susceptibility of the channel and also a permanent growth.[4]

6. When several channels are open to a nervous discharge, the discharge will be divided among the channels in proportion to the susceptibility at the time.

In order to save space no attempt will here be made to prove the reasonableness of the above premises. It is proper to say, however, that in the main they are in accord with the statements of writers of authority as will be found on consulting well known works on the subject.[5]

It may help some thinkers to form a clear idea of the effect of the time interval between discharges upon the susceptibility of the channel if we present it in the shape of a formula:

Let

CT	=	Combined present capacity of all channels
C_1	=	Present capacity of the given channel
CP	=	Original capacity of the given channel plus the permanent increase made by previous discharges.
CL	=	Temporary additional capacity of the given channel at the last discharge
t	=	Time since the last discharge through the given channel

[3] Thorndike, E. L. Animal Intelligence. New York, 1911, pp. 44, 249.
Meyer, Max. Fundamental Laws of Human Behavior. Boston, 1911, p. 86.
[4] Meyer, Max. Fundamental Laws of Human Behavior. Boston, 1911, p. 129.
[5] Special reference should here be made to the recently published book of Professor Meyer, Fundamental Laws of Human Behavior, for the reason that his argument is not altogether unlike that of this article. The writer will not presume to pass judgment on the book further than to say that in spite of its illuminating and most suggestive exposition it leaves room for further elucidation of the matter in hand.

e   = Unknown exponent
a & b = Unknown constants
F_I = Discharge through the given channel
FT   = Discharge through all channels

Our present capacity is then from premises 2, 3 and 4

$$C_I = CP + CL + a - bt^e$$

and from premise 6 we have

$$\frac{F_I}{FT} = \frac{C_I}{CT}$$

Having now a conception of how the susceptibility of a nervous channel will increase with each discharge and decrease with disuse, let us take up the problem of inhibition again. We will now modify our diagram so as to give this (Figure 002):
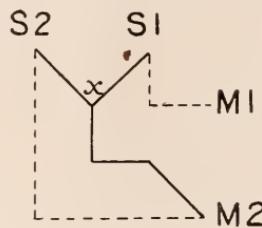
FIGURE 002

As before, S_I, M_I and S_2, M_2 are channels of good conductivity. The median channel S_I, S_2, x, M_2 is one originally of low conductivity. Now let the environment be such that the movement M_I habitually produces the sensation S_2.

From our premises we see that at each experience the susceptibility of channel S_I, S_2, x, M_2 is increased because its first discharge is followed quickly by a second. It is evident that the median channel will, after repeated experiences, become of high conductivity so that eventually the sensation S_I will be followed either by movement M_2 or at least by a prevention of M_I which is inhibition, as the movements are opposed.

We now see how experience can develop the weak channel faster than the strong one. This case may be considered as one of converging nervous channels.

To illustrate the case: the sight of the fire excites a forward movement, M_I. The sharp pain of the burn excites a back-

ward movement, M2. After repeated experiences the sight of the fire no longer excites a forward movement.

Let us now pass to the problem of association of ideas. The diagram given here will illustrate it (Figure oo3). Ma and Mb represent movements not opposed to each other.

As before, the channels Sa, Ma and Sb, Mb are of high conductivity while the median channel Sa, Sb, x, y, Ma, Mb is originally of low conductivity so that before experience the sensation Sa is followed only by the movement Ma and the sensation Sb is followed only by the movement Mb. Now let the environment be such that the sensation Sa is always succeeded quickly by Sb or vice versa. The discharge through the median channel Sa, Sb, x, y, Ma, Mb will be greater at each experience from our premises as in inhibition so that after a number of experiences the sensation Sa (or Sb) will result in
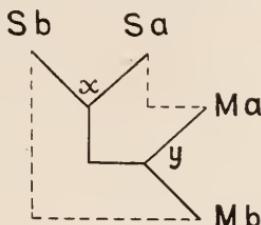
FIGURE 003

both movements Ma and Mb. Again the weak channel has grown faster and overtaken the strong ones. Eventually the originally weak channel will have dwarfed the others and for either sensation the discharge will be practically equal at Ma and Mb.

This case we may call one of diverging nervous channels. In it may be found the physiological accompaniment of the association of ideas.

As an illustration: the crack of the whip (Sa) makes the young horse prick up his ears (Ma); the sting of a blow makes him jump forward (Mb). If the blow often follows the sound, the jump will after a while be excited by cracking the whip. The ideas of the sound and the pain have become associated as the psychologist would say.

Looking at the problem from a quite different point of view for a moment, we may picture our nervous channels as chains or groups of neurons, each neuron being an individual organism.

A group of neurons may be likened to a colony of animals having points of contact with each other. Each neuron will resemble a wriggling animal with arms like an octopus. If any one animal is disturbed and made to wriggle, its movements are communicated to the adjoining animals which are disturbed and wriggle in turn. When the external disturbance ceases the animals gradually come to rest, then as gradually sink into sleep. The more often a given animal is irritated the more irritable he becomes. Disturbances will be conveyed through a colony on certain lines determined by experience. In a similar manner are disturbances transmitted through a nervous system.

Having given the above brief outline of a theory for the working of nervous discharges, a few words as to its significance may not be amiss. Present day explanations of the working of nervous discharges are so inadequate that they are helpful to few. They leave large gaps to be filled by the imagination.

A clear understanding of the working of the nervous system that would reach the great body of world students and be as lucid as the modern demonstration of the circulation of the blood would be a great acquisition to the cause of general education.

That such a clear understanding will some day be reached is most probable. It must be approached step by step. The step aimed at here is the first that naturally presents itself, for we find that a simple nervous discharge following a well defined channel as in simple reflex action, presents no difficulty to the scientific mind. The first step is then to explain such operations as learning, inhibition and habit forming. If we can make these clear to interested minds a barrier will be passed. That there will be other barriers to cross before animal intelligence is fully understood goes without saying.

The significance and importance of a proper solution of the problem can not be better stated than in the words of that high authority, Dr. Loeb,[6] viz.:

"The unravelling of the mechanism of associative memory is the great discovery to be made in the field of brain physiology and psychology."

[6] Loeb, J. Comparative Physiology of the Brain and Comparative Psychology. New York and London, 1900, p. 14.

The working of nervous systems has been viewed by science mainly in two aspects. First, the physiologists have studied their structure, growth and functions by dissection and experiment. Secondly, experimenters in the laws of animal behavior have gathered data of value from scientific observation. Under the same head might be put facts generally known about the training of animals and the teaching of young children. Our knowledge of the effect of time and of repetition in modifying nervous action is derived mainly from the sources under the second head.

It is thought that the engineering profession has not contributed greatly to the study of nervous systems, at least since Herbert Spencer, an engineer, wrote his book on psychology. As the co-operation of workers in different fields of knowledge is necessary in these days of specialists it may be argued that engineers can consistently join in the consideration of a subject of such importance to man. As a member of the engineering profession then, the writer is not without excuse for advancing ideas on the working of nervous systems for the consideration of physiologists and others who have knowledge of the matter.

In discussing the subject of this article diagrams are necessary and demand no apology. To many minds the explanation here given of the modification through sensory experience of nervous channels may be clear enough and even sufficiently convincing. It is thought, however, that the hypotheses advanced could be made more convincing to others if they were embodied in a practical mechanical device such as could be built and operated. This device would simulate the working of nervous discharges by purely mechanical means. With it, one could demonstrate the modification of action or behavior by experience.

<div align="center">OPERATION</div>

Figures 1, 2, and 3 show the construction to be used with compressed air or hydraulic pressure. In this description it will be assumed that hydraulic pressure is used.

In figure 1 the slide valve 6 is shown at the extreme end of its inward stroke as in receiving a signal. This valve, known as the spur valve, when in this position, opens ports 4 and 5 on the pressure side. The spur valve spring 7 is now compressed. The pawl 8 which is attached to the spur valve, is
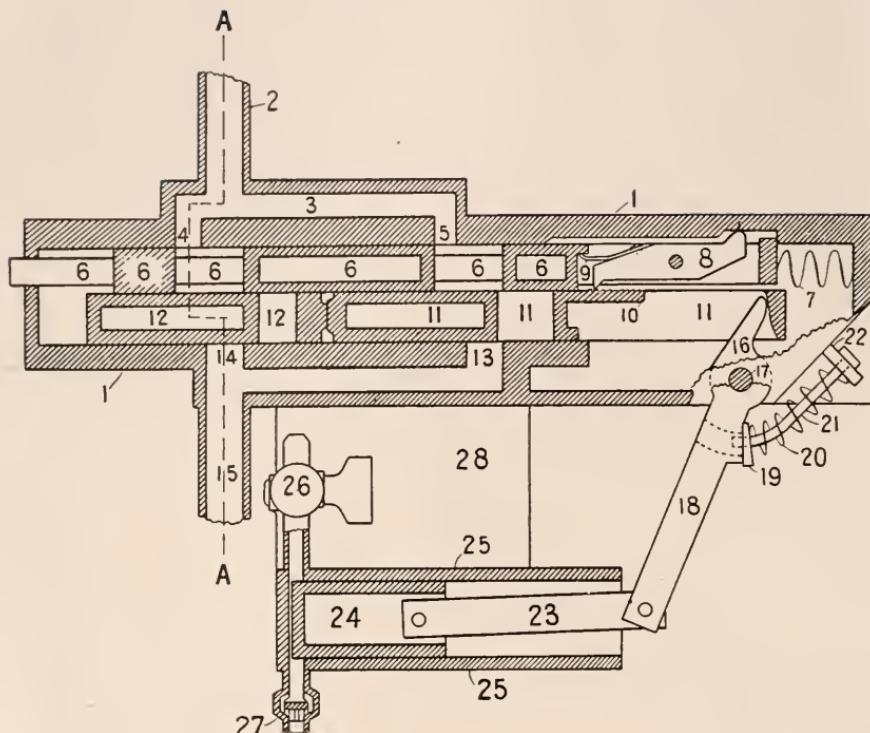
FIGURE 1. Transmitter. Longitudinal section on line B B of Figure 2

REFERENCE NUMBERS

FIGURES 1-4

1 Transmitter case
2 Pressure pipe
3, 4 and 5, Pressure ports
6 Spur valve
7 Spur valve spring
8 Pawl
9 Pawl spring
10 Ratchet
11 Ratchet valve
12 Lag valve
13, 14 Issue ports
15 Meter pipe
16 Rocking finger
17 Finger shaft
18 Finger lever
19 Washer
20 Lever spring
21 Guide pin

22 Spring lug
23 Connecting rod
24 Plunger (dash pot)
25 Dash pot barrel
26 Adjusting cock
27 Check valve (dash pot:
28 Bracket (dash pot)
29 Main pressure pipe
30, 31 Collecting pipes
32, 33 Meter cones
34, 35 Meter discs
36, 37 Guides
38 Meter stem
39 Meter link
40 Rocking lever
41 Connecting rod
42 Slide valve rod
43 Balanced slide valve
44 Valve chamber

45 Cylinder
46 Piston
47 Piston rod
48 Cylinder barrel
49 Exhaust port
M1 and M2 Admission ports
50 and 52 Exhaust passage
51 Pressure pipe
53 Exhaust outlet
S1n, S3n, S5n, S2n, etc. Transmitters
115, 116 Key Rods (S1 and S2)
117, 118, 119 Spur rods
120, 121 Bell cranks
122 Suspender links
123 Coupling gang frame

held down on ratchet 10 by the pawl spring 9 so as to engage it. Valve 6 slides over the lag valve 12 and the ratchet valve 11.

The ratchet valve 11 is shown in the figure in its original position or right hand end of its stroke. When valve 6 is permitted to make its return or outward stroke the valve 11 moves also, pushed by the pawl 8. If valve 6 has a stroke of one and one-half inches, valve 11 will move with it about one-fourth inch. The lag valve 12 will also move the same distance pushed by valve 11. When one-fourth inch of the return stroke has been made, pawl 8 is tripped by the striking of the lug on top of the pawl against a shoulder in casing 1. When the ratchet valve is thus released, it moves to the right, driven by lever spring 20 acting through finger lever 18, finger shaft 17 and rocking finger 16. When ratchet valve 11 moves to left it acts through the said finger lever, etc., together with connecting rod 23 so as to draw out dash pot plunger 24 and thus suck air (or water) through check valve 27. When, on the other hand the ratchet valve moves to the right, the dash pot plunger is driven back by the action of lever spring 20. The air now contained in dash pot 25 is prevented from escaping by check valve 27 and can only pass out through adjusting cock 26. In this way the return stroke of ratchet valve is retarded and is very slow. When ratchet valve moves to right on its return stroke it leaves the lag valve 12 behind.

If the time interval before a second stroke of spur valve 6 is long enough, ratchet valve 11 will have reached its original position and its second stroke will be the same as the first and lag valve 12 will not be moved. If on the other hand, the time interval is short so that the second stroke of the spur valve comes before the ratchet valve has arrived at its original position, the ratchet will cause the ratchet valve to advance further to the left than before and hence the lag valve will be advanced further to the left.
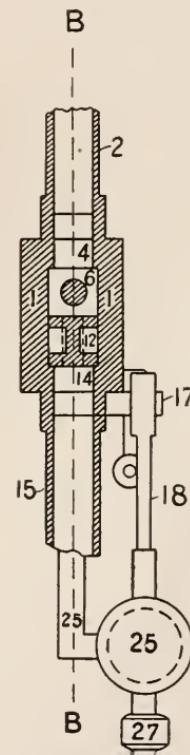
FIGURE 2. Transmitter. Transverse section on line A A of Figure 1.

Now, the further valve 11 moves to the left the greater will be the effective opening for water from pressure port 5 to issue port 13. Hence the effective opening at any stroke will be in inverse proportion to the time interval since the previous stroke. In other words the passage way will gradually close between strokes.

In the case of the lag valve 12, the further it moves to the left the greater will be the effective opening for water from pressure port 4 to issue port 14. As this valve always moves to the left, it will be seen that the effective opening through valve 12 is proportional to the maximum previous opening of the ratchet valve.

The combined effective area of valves 11 and 12 gives the effective area of the transmitter, and it will be seen that this area is susceptible to increase two ways, viz., temporary increase by valve 11 and permanent increase by valve 12. A rapid succession of strokes of the spur valve will cause a decided increase of opening through the transmitter and hence a decided increase in the discharge through the same when open. The hydraulic pressure in pressure pipe 2 is assumed to remain constant.

It will be noted that when the spur valve is in its outward position all ports are closed and there is no discharge through the transmitter. When the spur valve is moved inward, however, it creates an opening the effective area of which depends on the position at the time of the ratchet and lag valves.

In other words, the transmitter is a valve whose maximum opening is variable and is determined by the frequency of operating. Between operations the maximum opening is automatically and gradually reduced.

In figure 3 several transmitters, S_1n, S_3n, etc., are shown connected so that their meter pipes 15 enter into a manifold pipe 31. There are also several transmitters, S_2n, S_4n, etc., similarly connected into a manifold pipe 30. In the figure the transmitters are shown in a horizontal line for the sake of simplicity. Of course, they will work just as well if arranged in vertical columns with proper connections. Collecting pipes 30 and 31 discharge into opposite sides of exhaust passage 52 through meter cones 32 and 33. The discharge from 31 through 33 impinges on meter disc 35 tending to move it to the right
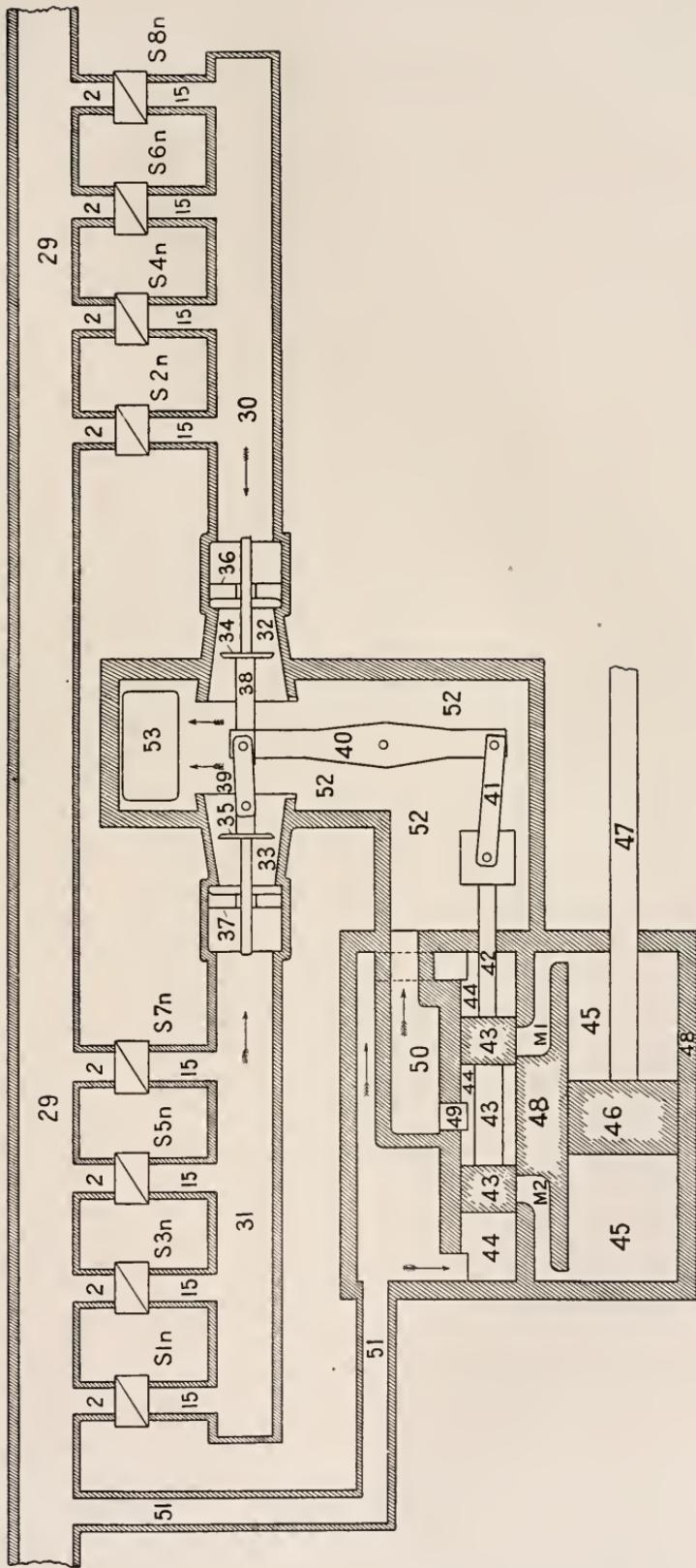
FIGURE 3. Stream meter, slide valve and cylinder. Longitudinal section.

while the discharge through 32 tends similarly to move meter disc 34 to the left. These discs are mounted on meter stem 38 which moves in guides 36 and 37. In figure 3 the meter stem is shown in mid position as it would be if the discharges from 30 and 31 were equal. Should the stream from pipe 30 become greater than the other the discs would take a position more to the left.

The position of the meter discs determines the position of slide valve 43 through the meter link 39, the rocking lever 40, the connecting rod 41 and the slide valve rod 42. The slide valve should be balanced so as to reduce friction. When it moves to the right it opens admission port M_2 to pressure from pipe 51 through chamber 44 and it opens port M_1 to exhaust passage 50 through 44 thus causing the piston 46 to move to the right. The slide valve ports, piston, etc., are of familiar construction.

The combination of discs, cones, etc., forms the *stream meter*. It will be seen that the stream meter controls the hydraulic cylinder. But the stream meter is controlled in turn by the transmitters that govern the tributary streams. If the sum of the streams from transmitters S_{2n}, S_{4n}, S_{6n}, and S_{8n}, be greater than the sum of the streams from transmitters S_{1n}, S_{3n}, S_{5n}, and S_{7n}, the piston rod 47 will move out. If it be less, the piston rod will move in. Now, the stream from a single transmitter is variable as has been shown, so that the stream from S_{2n} alone may be greater than the added streams from S_{1n} and S_{3n}. From this it may be seen that if the transmitters S_{1n}, S_{3n}, and S_{2n} are opened simultaneously, the movement of the piston rod may be either outward or inward according to the frequency with which S_{2n} has previously been operated.

By the system above described we see that we have a hydraulic cylinder that is subject to the control of any one of its transmitters and also to a variety of combinations of transmitters working in concert, the result in each case depending largely upon what might be called the "experience" of the transmitters in the combination.

The system described is for use with hydraulic pressure or compressed air. An equally practical system which will not here be described is for use with electric control, i.e., with elec-

tric transmitters and with electro magnets controlling the slide valve of the hydraulic cylinder.

Figure 4 shows the construction of a *coupling gang* which is an appliance for working groups of transmitters in combination. In this particular coupling gang there are 5 transmitters operated by two key rods. Each key rod opens 3 transmitters. When a key rod is moved downward the motion is communicated through the connecting bell-cranks to the spur rods which move horizon-
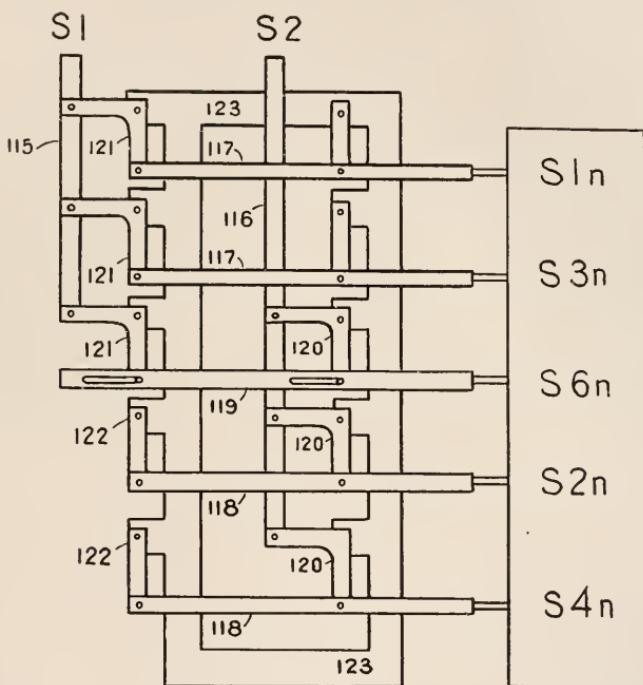
FIGURE 4. Side view of a coupling gang for 5 transmitters.

tally. Spur rod 19 for transmitter S6n is moved by either key rod by means of slotted holes for the bell-crank pins. Each spur rod pushes against and works the spur valve of a transmitter.

It is evident that a coupling gang on this order may be used to control all the transmitters of a given stream meter. Or a coupling gang may be used to co-ordinate the movements of several hydraulic cylinders through their respective transmitters and stream meters.

To show how different forms of coupling gangs may be employed, diagrams of two arrangements are shown in figures 5 and 6 and tables are used for others. In figure 5 the left hand diagram FL known as a stream diagram shows diagrammatically the form of the hypothetical channels that connect the sensory terminals SO, SD and SL at the top of the diagram with the motor terminals MO, MD and ML at the right of the diagram. The broken lines show the direct channels that prevail at first. The solid lines show the channels that are devel-
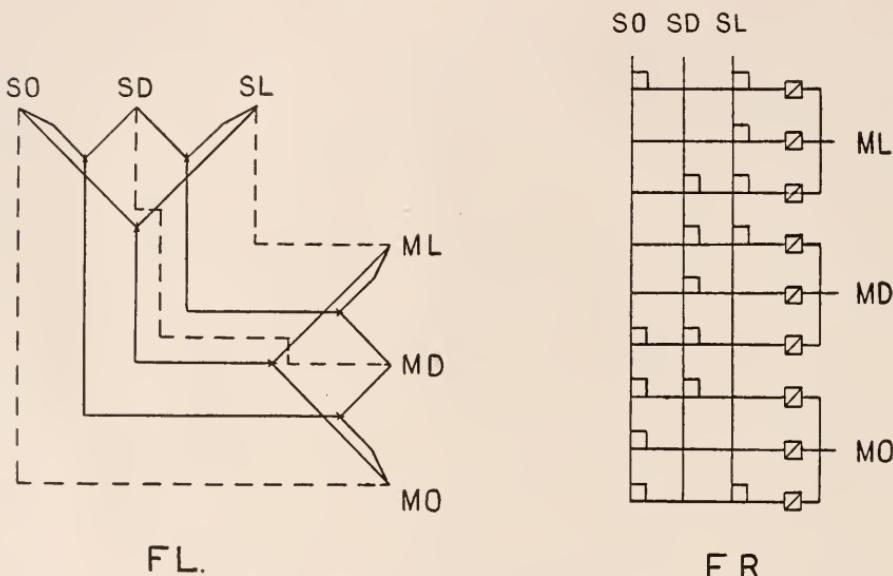
FIGURE 5. Coupling diagram and stream diagram for a 3-way diverging gang of 9 transmitters.

oped by favorable experience. Figure 6 shows a similar stream diagram referred to again later.

In figure 5 the right hand diagram FR, known as a coupling diagram, shows how the key and spur rods are arranged and connected so as to work the transmitters. The key rods are represented by vertical lines and the spur rods are shown by horizontal lines. The bell crank connections to be used are indicated. A single transmitter connected to one key rod corresponds to a direct channel. Two transmitters connected to the same two key rods correspond to a diverging channel. Each

transmitter is indicated by a square with diagonal line. The pipe lines connecting the transmitters into groups are indicated by connecting lines on the right. Each group of connected transmitters will act as one, on a certain stream meter controlling a hydraulic cylinder. The meters and cylinders are not shown.

In the case of figure 6 no coupling diagram is given but the arrangement of the rods and connecting bell cranks is adequately shown in tabular form in table III. Each key rod is represented by a column and each spur rod by a row. B.C. at the intersection indicates a bell crank connection. x1, x2 and x3 refer to corresponding connections in figure 6. The motor connections are in the right hand column. Sn in the next column indicates a transmitter. Other forms of coupling gangs are shown by means of tables similar to table III. No stream diagrams are shown for some of these arrangements but one could readily be constructed from each table by aid of figures 002, 003, 5 and 6. We will now take up briefly each form of coupling gang, beginning with the simplest.

In table I is represented a converging gang which may be used like that shown in figure 4 to illustrate the theory for in-

TABLE I (Fig. 002)

CONVERGING GANG

Key Rods			Movement
S 2	S 1		
—	B.C.	S n	M 1
B.C.x	B.C.x	S n	M 2
B.C.	—	S n	"

TABLE II (Fig. 003)

DIVERGING GANG

Key Rods			Movement
S b	S a		
—	B.C.	S n	M a
B.C.	B.C.	S n	"
B.C.	B.C.	S n	M b
B.C.	—	S n	"

hibition as explained previously. Table II represents a diverging gang to illustrate the association of ideas as explained.

Figure 5 shows how three movements, MO, MD and ML, may be so co-ordinated that one key rod can, after the required experience, cause three cylinders to move together where originally only one of the cylinders was started by the said rod.
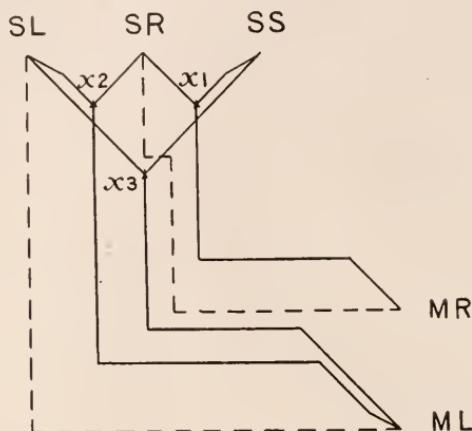
FIGURE 6. Stream diagram for a duplex converging gang.

Figure 6 and table III show a duplex converging gang. In this arrangement the first key rod (or sensory terminal) SS is known as the station key. MR and ML are opposite movements. If SS and SL are habitually struck in succession except when SS, SR and SL are struck in succession the device will become "trained" so that when SS is struck the move-

TABLE III (Fig. 6)

Duplex Converging Gang

Key Rods				Movement
S L	S R	S S		
—	B.C.x1	B.C.x1	S n	M R
—	B.C.	—	S n	"
B.C.x2	B.C.x2	—	S n	M L
B.C.x3	—	B.C.x3	S n	"
B.C.	—	—	S n	"

ment ML will result. On the other hand if SS and SR are habitually struck in succession the key SS will when struck give the opposite movement MR.

TABLE IV

6 Way Diverging Gang of 24 Transmitters

Key Rods							Movement
S U	S D	S L	S R	S O	S I		
B.C.	—	—	—	—	B.C.	S n	M I
—	B.C.	—	—	—	B.C.	S n	"
—	—	B.C.	—	—	B.C.	S n	"
—	—	—	B.C.	—	B.C.	S n	"
B.C.	—	—	—	B.C.	—	S n •	M O
—	B.C.	—	—	B.C.	—	S n	"
—	—	B.C.	—	B.C.	—	S n	"
—	—	—	B.C.	B.C.	—	S n	"
B.C.	—	—	B.C.	—	—	S n	M R
—	B.C.	—	B.C.	—	—	S n	"
—	—	—	B.C.	B.C.	—	S n	"
—	—	—	B.C.	—	B.C.	S n	"
B.C.	—	B.C.	—	—	—	S n	M L
—	B.C.	B.C.	—	—	—	S n	"
—	—	B.C.	—	B.C.	—	S n	"
—	—	B.C.	—	—	B.C.	S n	"
—	B.C.	B.C.	—	—	—	S n	M D
—	B.C.	—	B.C.	—	—	S n	"
—	B.C.	—	—	B.C.	—	S n	"
—	B.C.	—	—	—	B.C.	S n	"
B.C.	—	B.C.	—	—	—	S n	M U
B.C.	—	—	B.C.	—	—	S n	"
B.C.	—	—	—	B.C.	—	S n	"
B.C.	—	—	—	—	B.C.	S n	"

This arrangement is of special interest, as with it we can simulate the working of nervous discharges in an animal learning the path around an obstacle. The key SS corresponds to the sensation arising from the situation. MR is turning to right. ML is turning to left. The animal after experience turns to the left we will say at the signal SS. The machine after similar experience acts similarly.

In table IV a 6-way diverging gang is shown without any diagram. By this arrangement three hydraulic cylinders may be controlled and thus we could govern movements in three directions as in and out, right and left and up and down. After suitable experience the striking of a single key rod would cause movement in two or three directions, as will be seen by a study of the table, if one remembers that the discharge from a transmitter increases when it is operated at short intervals.

Table V represents a tandem converging gang. S_1, M_1, and SR_1, MR and SR_2, MR correspond to channels originally of high conductivity, (first, fourth and fifth rows), while S_1, SR_1, MR and S_1, SR_2, MR corresponds to channels originally of low conductivity. Now let the environment be such that the sensation S_1 is soon followed by the sensation SR_1 and such that the response MR brings about a sensation SR_2, it will be seen that the channel S_1, SR_1, MR and the channel S_1, SR_2, MR (second and third rows) will grow at each experience and the result will be that the signal S_1 will be strongly connected to the response MR or in other words that the transmitters in the second and third rows of the table will give increased discharge.

TABLE V

Tandem Converging Gang

Key Rods				Movement
S R 2	S R 1	S 1		
—	—	B.C.	S n	M 1
—	B.C.	B.C.	S n	M R
B.C.	—	B.C.	S n	"
—	B.C.	—	S n	"
B.C.	—	—	S n	"

This mechanism is of especial interest as it illustrates the physiological accompaniment of a form of satisfaction, showing how associations may be reinforced or stamped in. Such satisfaction we may say is the antithesis of inhibition.

To explain, it is thought that where the situation is such that a given response is followed by a new or changed sensation which gives the same response the effect is a form of satisfaction. To illustrate this, if the puppy is induced to suck the teat and the sucking results in a pleasant taste which causes him to suck harder, that is satisfaction.

The signal SR_2 in table V belongs to a class that may be known as counter signals. A counter signal is a signal (or sensation) that is due to the reaction of the environment to a given motor response. A counter signal may be inhibiting or reinforcing or otherwise according to the structure of the nervous channels (or coupling gang). For example, the whine of the infant is a motor response and its counter signal is the offer of the nipple. The sucking is a motor response and its counter signal is a pleasant taste. S_2, table I, is also a counter signal. Counter signals or sensations play an important part in the development of nervous channels as has been shown for simple cases of inhibition and satisfaction. It is largely through the effect of counter signals on the nervous system that it is brought into proper correspondence with the creature's environment.

It is evident that the forms that we have illustrated in the figures and tables could be combined in various ways so that many types of response to situation could be simulated. For example, the arrangement shown in table V may be modified by adding two more key rods on the left and four more transmitters. By suitable connections we will have a two way tandem converging gang which will simulate the selection of responses by satisfaction. Whatever system of coupling be employed to control a plurality of movements there will be found the same general principle throughout. Along with the description we have incidentally observed how the mechanical action simulated particular nervous developments. As to general analogy of the apparatus with a nervous system we may briefly note:

A 1, A simultaneous flow in several meterpipes results in a certain movement or movements.

A 2, A simultaneous flux in several nerves results similarly in a certain movement or movements.

B, The effect of time intervals between discharges in determining variation of response is the same in the apparatus as it is in a nervous system.

Of course there are types of response to environment that are not covered by this discussion. It is believed, however, that the theory advanced herein with some modifications will be found to answer for a large part of the field which is not included.

In reviewing the different arrangements shown in our tables and diagrams one fact seems to be brought into prominence. It is that the channel that is to be made to govern after suitable experience must be there in the first place as part of the structure. In regard to nervous systems this is not such a great difficulty as it may seem. Remember the shocking stupidity often shown by animals usually thought intelligent and the limited field in which animals can be trained. On the other hand there is reason to think that in life many nervous channels remain undeveloped. Moreover there is abundant evidence in animal behavior to show that the associative memory of each species is in proportion to the complexity of its nervous system.[7]

Our mechanical system may be thought at fault because it requires signals to succeed each other in order to affect the opening of the transmitters, so that if two sensations were simultaneous they would never become associated together.

The answer is that each of two simultaneous signals may be associated with a common signal which precedes them.

To summarize briefly the points covered we have shown that a comparatively weak nervous channel may become a comparatively strong one if it be provided with two sensory points and with outside occurrences that shall cause the two points to be excited in succession from time to time. We have shown how this principle will account for the different ways of learning and habit forming.

We have also demonstrated a mechanism that will simulate in its various forms the working of nervous discharges. With

[7] Loeb, J. Comparative Physiology of the Brain and Comparative Psychology. New York and London, 1900, p. 13.

it, as in a nervous system, we find that as a result of individual experience, changes take place so that with the same signals as before the responses have changed and vice versa we find the same responses when the signals have changed. We have a mechanism that can be trained, that can acquire habits, that will move either forward or back at a given signal according to experience, that will make one, two or three responses to a given signal according to experience.

In other words we have shown a practical arrangement of mechanical transmitters and receivers that will respond to signals and control movements like a nervous system and that possesses associative memory as it can learn by experience. For, quoting Dr. Loeb again, "If an animal can be trained, if it can learn, it possesses associative memory."

THE BEHAVIOR OF A PARASITIC COPEPOD, *LERNAEOPODA EDWARDSII* OLSSON

NATHAN FASTEN

Zoölogical Laboratory, The University of Wisconsin

CONTENTS

I. GENERAL REMARKS

The data presented in this paper were obtained during July and August of 1912, while the author was in the service of the Wisconsin Fish Commission, studying an outbreak of parasitic copepods in the trout hatchery at Wild Rose, Wis. The brook trout, *Salvelinus fontinalis*, were found to be attacked by the copepod *Lernaeopoda edwardsii*. Most generally this parasite attaches itself to the filaments of the gills, but sometimes it is found on the gill operculum, the roof of the mouth, and on the pectoral and pelvic fins. For its identification, I am indebted to Professor C. B. Wilson. To the Commissioners of Fisheries of the State of Wisconsin, and their employes, especially Mr. Zalsman, foreman of the Wild Rose hatchery, my thanks are due for many courtesies shown me. To Professors E. A. Birge, George Wagner, and A. S. Pearse I wish to extend my best thanks for their many helpful suggestions.

II. DESCRIPTION OF THE FREE-SWIMMING COPOPOD

Lernaeopoda edwardsii, like all known species of the *Lernaeopodidae*, is parasitic during almost its whole life. The dura-

tion of its free-swimming existence is very short, perhaps not more than two days. Its nauplius and metanauplius stages are passed within the egg sac of the mother, and the animal hatches
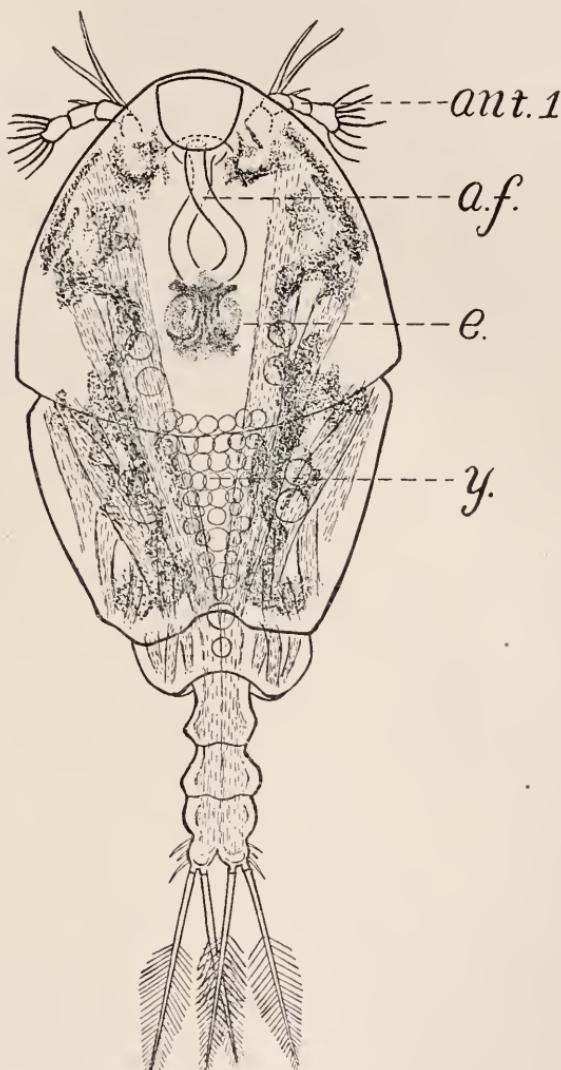
FIGURE 1.   Lernaeopoda edwardsii.   Dorsal view, free swimming stage, x 173.5
a. f.   =attachment filament.
ant. 1=first antennae.
e   =x-shaped eye.
y   =yolk.

into a fully developed larval form, which immediately begins
an active hunt for its host. During this stage of its life history
the copepod does not feed, its nourishment being derived from
the yolk which it carries over from its embryonic development
(figure 1, y).

The larva is minute in size, about 0.726 m. m. in length.
Running along each side of its dorsal surface are two well de-
fined brownish streaks of pigment. A characteristic x-shaped
copepod eye occupies the middle of the head (figure 1, e).

The head is broad, elliptical, and bears the mouth parts and
a peculiar attachment filament. The mouth parts are situated
on the ventral surface and consist of the first antennae, the
second antennae, the mouth tube, stationed between the second
antennae, the mandibles, the two pairs of maxillae (the first
and the second), and the maxillipeds. The attachment filament
is located beneath the head, and is made up of two parts:—
(1) a broad circular, mushroom-like body whose position is
between the first antennae, and (2) a tube-like structure, which
makes its way backward from the posterior region of the mush-
room body as far as the eye, and then turns upward in one
circular loop, passing underneath the first part of the tube, and
continues to ascend until it reaches the level of the posterior
margin of the mushroom body, where it is attached to the
head (figure 1, a, f).

The thorax has two segments and these bear the two biram-
ous swimming feet (Fig. 2 s. f. 1 and s. f. 2), which end in broad
laminated bases—the respective exopods and endopods. Each
exopod terminates in four long feathery setae, whereas the
endopods contain seven of these plumose structures. The feet
are operated by a system of strongly developed dermal muscles
situated along the dorsal side of the body.

The abdomen is rather slender and contains three segments.
The last of these is supplied with four feather-like setae, as
well as three pairs of smaller seta-like appendages, that are
vestigial in character.

The head and the first thoracic segments comprise the main
bulk of the copepod's body. Figures 1 and 2 illustrate, respec-
tively, a dorsal and a ventral view of the free-swimming copepod.
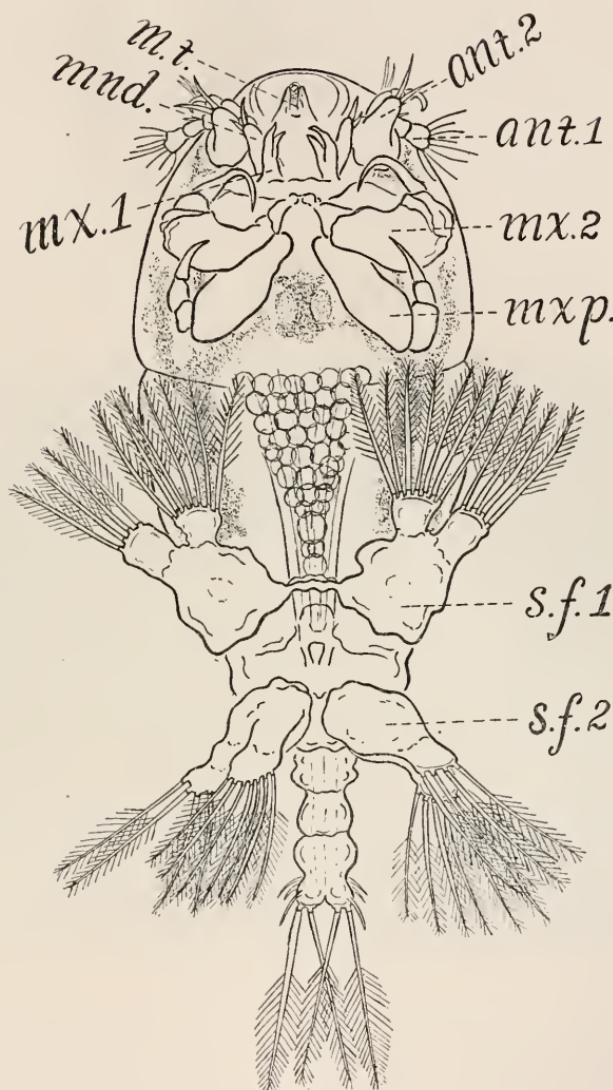
FIGURE 2. Lernaeopoda edwardsii. Ventral view, free swimming stage, x 173.5
ant. 1=first antennae.
ant. 2=second antennae.
mnd. =mandibles.
m. t. =mouth tube.
mx. 1=first maxillae.
mx. 2=second maxillae.
mxp. =maxillipeds.
s. f. 1=first pair of swimming feet.
s. f. 2=second pair of swimming feet.

III. HATCHING THE ORGANISM

In order to obtain enough material for experimentation, it became necessary to hatch the copepods artificially. The first efforts were confined to attempts to hatch the parasites in aquaria within the hatchery, but this proved a failure. Conditions here were far from normal, and the attempt was soon abandoned.

Outdoor experiments were next tried. Two large tanks were constructed, which were eight feet long by three and one-half feet wide and two and one-fourth feet high. The frame of
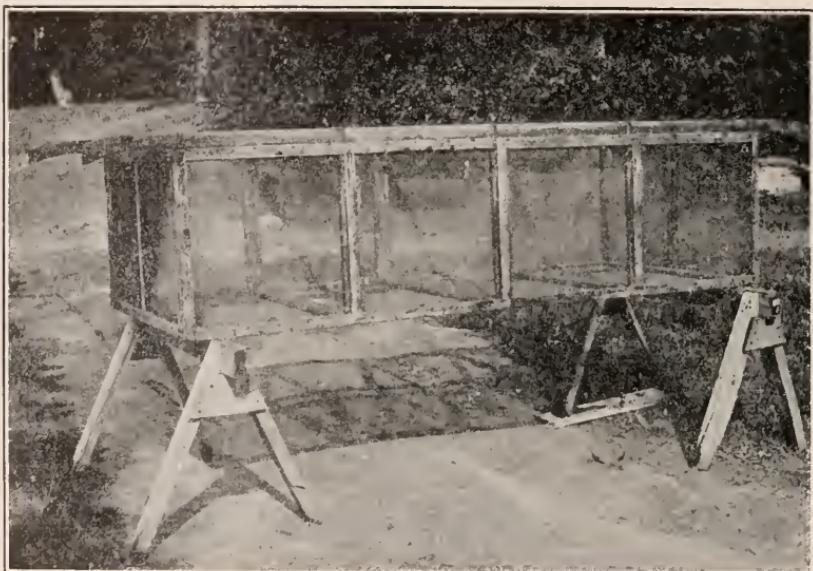
FIGURE 3.   Hatching tank

these tanks was made of wood, while the sides consisted of coarse wire netting. The interior faces were lined with fine linen gauze so as to prevent the escape of any copepods. Figure 3 is a photograph of one of the tanks.

Simply stationing these tanks in one of the open hatchery ponds proved insufficient, for, through lack of circulation, trout placed into them very quickly succumbed. So the tanks were placed in such a way that the water from some feed pipes ran directly into them. This arrangement proved entirely satisfactory. Figure 4 shows the manner in which the tanks were

placed within the pond. The water can also be seen entering them.

Before putting any of the infected fish into the tanks, the water in the feed pipes was thoroughly examined in order to determine whether *Lernaeopoda edwardsii* existed in it. Fine linen bags were tied over the outflows, thereby catching the organisms brought in by the water. The contents of these bags were looked over under the microscope three times daily. Fifteen examinations of these catches did not reveal a single
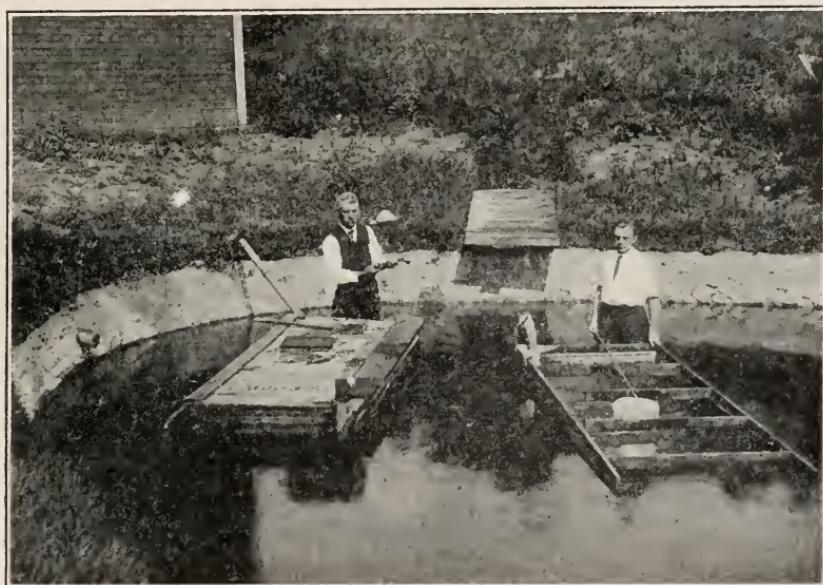
FIGURE 4. Tanks in position

parasitic copepod, and this convinced me that the water was free from the infection. One hundred parasitized trout were next introduced into each tank, and the covers placed over them. Two days later, the first batch of free swimming larvae was obtained—about two dozen of them. This was on July 17th, and almost every day after that until September 5th, when the investigator left the hatchery, from a dozen to three dozen free swimming parasites were secured.

The animals were scooped up with an open tow net, which was dragged along the surface of the water. The net had an aluminium cup attached to its tapering end. In the bottom of

this cup there was an opening covered by a tightly fitting screw-cap. By unscrewing this cap, each haul could easily be transferred from the cup to another receptacle without losing any of the gathered organisms. Generally, each catch was strained through a fine linen plankton sieve, in order to condense the haul for examination. By means of a pipette the copepods were segregated from the other organisms, and introduced into a clean dish of water, where they were allowed to remain until needed.

IV. MOVEMENTS OF THE LARVAE UNDER NORMAL CONDITIONS

In the free living stage, the copepod swims about actively, with a snappy, dart-like spiral motion. Its mouth parts are, at the same time, moving incessantly, always ready to grasp their host and thereby insure the further development of the organism. Movement through the water is accomplished by the two biramous swimming feet on the thorax. In their normal resting attitude, the feet are held in an oblique position, with their setae pointed toward the head of the organism. The abdominal portion of the copepod is somewhat bent, at an angle of about 20° with the long axis of the body.

Motion is produced by the contraction of the powerful dermal muscles, which cause the swimming feet to dart backwards, thus shooting the organism ahead. The copepod, in its motion, passes through the same angle as that which the swimming feet traversed in the act of propelling the body. The actual distance covered by the copepod through one stroke of its feet is about an inch. Further motion is accomplished by a repetition of the same process; the animal thus travels in a snappy, spiral path (figure 5). When motion ceases, Lernaeopoda usually takes an upright position, with its long axis almost perpendicular to the surface of the water. Soon it turns upside down, and slowly begins to sink to the bottom, where it may assume a ventral or a dorsal position, depending entirely on which side of the body strikes the bottom first.

Oftentimes the copepod is found adhering to the side of the glass dish nearest the window, or it may sometimes suspend itself on the surface film of the water. In such cases, the larva maintains an upright position, while the first antennae are stretched out horizontally, making an angle of almost 90° with

the long axis of the body. By means of these antennae the copepod is enabled to cling to the sides of the dish or to suspend itself from the surface film. In the latter case, surface tension undoubtedly plays the important rôle in maintaining the animal. Parker (1901), has observed similar behavior in the marine copepod *Labidocera aestiva*. He concluded that the antennae serve as means of attaching the copepod to fixed objects or to the water film. My observations are in accord with his.

The peculiar spiral movement of the copepod is of great significance. Many of the Protozoans and Rotifers have for a long time been known to move in this way. Jennings, more than any other investigator, has made a careful study of the
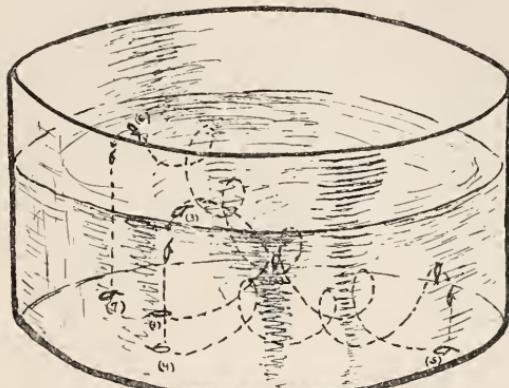
FIGURE 5.   Normal movements of larva.

problem, and has shown that a spiral path is of great adaptive value to the lower organisms. He has found (1901, '04, '06) that most of the Infusorians, especially the "hunter ciliates," move in a spiral course. In his work on Paramecium we get a thorough analysis of this type of locomotion. Discussing the adaptiveness of this movement, Jennings says:

"The problem solved by the spiral path is as follows: How is an unsymmetrical organism, without eyes or other sense organs that may guide it by the position of objects at a distance, to maintain a definite course through the trackless water, where it may vary from the path to the right or to the left, or up or down, or in any intermediate direction? It is well known that man does not succeed in maintaining a course under similar

but simpler conditions. On the trackless, snow-covered prairie, the traveler wanders in circles, try hard as he may to maintain a straight course, though it is possible to err only to the right or left, not up or down as in the water. Paramecium meets this difficulty by revolution on the axis of progression, so that the wandering from the course in any given direction is exactly compensated by an equal wandering in the opposite direction. Rotation on the long axis is a device which we find very generally among the smaller water organisms for enabling an unsymmetrical animal to follow a straight course. The device is marvellously effective, since it compensates with absolute precision for any tendency or combination of tendencies to deviate from a straight course in any direction whatsoever."

"The normal movements of Paramecium are adaptive in another respect. The same movements of the cilia, which carry the animal through the water, also bring it its food. Thus Paramecium is continually receiving samples of water in front of it. Since in its spiral course the organism is successively pointed in many different directions, the samples of water it receives likewise come successively from many directions. The animal is given opportunity to try the various different conditions supplied by the neighboring environment."

In the case of Lernaeopoda, we meet with a similar condition. The organism, like Paramecium and the other Infusorians, circles through the water in its characteristic way, "trying" the water, so to speak, in every direction. Of course, the animal being a parasite throughout most of its life, must come in contact with the proper host in order to carry on its further development. In other words, the copepod, like Paramecium, must meet its food in order to exist.

It is questionable whether the larva perceives objects through its ocellus. Even if it did, however, the visual range would, in all probability, be so short that the organism could not see its host in the water. It thus becomes a question of the copepod searching out its host by random movements, or perishing. Chance plays the greatest part in its ever meeting the host. The movements of the animal, therefore, are apparently adaptive. The copepod darts up and down, circles in this direction and in that. Its movements bring it into as many different localities as possible. If one path happens to bring it in con-

tact with the necessary host, attachment immediately takes place, and the life of the individual and its progeny is secure. If, however, the organism does not meet the host, it tries other regions. The copepod perishes if its movements do not meet success within a given time.

V. REACTIONS TO CONTACT

Lernaeopoda is often found adhering to small bits of alga and other substances that float about loosely in the water. A glass rod or a needle may be slowly brought in contact with the body of the copepod, without producing the avoiding reaction. The organism may even adhere to the object for some period. When an object rapidly approaches the animal, it immediately shifts its position, thus avoiding the obstacle. Tapping or jarring a dish containing the copepod, even blowing on the surface of the water, or allowing a drop of water to fall directly above a resting copepod, calls forth the avoiding response; the animal quickly leaves its initial position and moves to other regions. When a copepod is picked up in a pipette and transferred to another dish of water, it almost always sinks to the bottom and remains motionless for a few seconds. Then it begins to dart about actively. In general, Lernaeopoda reacts positively to contact stimuli which are weak in character, whereas to strong stimuli it is negative.

VI. REACTION TO GRAVITY

Normally, Lernaeopoda responds positively to gravity. Its specific gravity is heavier than that of water, and it therefore tends to sink to the bottom. This was determined by the following experiment. Six copepods were placed in a test-tube filled with water and this was then tightly corked. When the tube was held in a vertical position, the organisms were observed to sink to the bottom, with their bodies almost vertical and their heads downward. As soon as they reached the bottom of the tube, the animals assumed a horizontal position, either ventral or dorsal, and began to move about actively. When the tube was reversed the larvae again sank to the bottom in their characteristic way. When the side of the test-tube was lightly tapped, while the copepods were passively sinking downward, they were observed to instantly dart upward again. How-

ever, as soon as the disturbing agent ceased acting, the animals
again began to sink, until they reached the bottom, and here
they moved about in their peculiar way. It becomes evident
that this is not exactly a case of geotactic response but merely
a result due to the high specific gravity of the copepod.

VII. REACTIONS TO LIGHT

1. *Behavior in daylight.*—Seven copepods were placed into a
round dish of water, and allowed to remain near a window for
some time. Soon all the organisms gathered near the window.
Rarely did one leave the area. If a copepod, through its motion,
happened to be brought into the opposite side of the dish, it
soon began to adjust itself accordingly, swimming about actively
until it was brought into the region of greatest illumination.

When a hand was passed between the window and the glass
dish, the shadow caused the copepods to momentarily dart
about. They did not, however, leave the most highly illumi-
nated side of the dish, but actively moved about in it. The
response in this case is similar to what Whitman (1898) has
observed in the leech Clepsine. If a hand is passed over a dish
containing a number of Clepsine, the shadow causes the animals
to stretch in every direction, as if trying to reach something.
Bateson (1887), has found that a passing shadow also causes
a similar response in shrimps and prawns.

Obviously, this mode of behavior is of great value in pro-
curing these animals their food. As Mast (1911) says, "The
important point is that the shadow in itself is of no particular
importance, but what follows may be."

In direct sunlight, the copepods were found to behave simi-
larly. The reaction was observed many times and the positive
phototropism was very striking.

2. *Behavior in artificial light.*—All experiments with artificial
light were carried on during the evenings. The hatchery was
situated a good distance from any of the neighboring dwelling
houses, and it was also surrounded by tall trees, so that the
laboratory was perfectly dark on the nights when experiments
were conducted.

Five copepods were placed into a circular dish, eight and
one-half inches in diameter, and this was allowed to remain
in darkness for about an hour. The current was then switched

on to a 60 c. p. Mazda bulb, which had previously been arranged in position about a foot from one side of the dish. When first illuminated, all the copepods were found to be at the bottom; but soon they began to dart about in every direction, ultimately making their way into the lighted area, where they remained. When the light was shifted to the opposite side of the dish, the organisms also changed their position. They moved about actively and in a few moments all had made their way across the dish, to the light side. An object, such as the hand, passed between the light and the dish, produced the same reaction as that brought forth by the shadow in ordinary daylight.

When an aqueous solution of alum was intercepted between the dish containing the free swimming copepods and the light, in order to absorb the heat from the rays, the organisms were found to behave similarly. Of course, the water in the dish served the same purpose to some extent. It is seen then that it is the light which causes the copepods to orient and not the heat produced by the electric bulb.

In another series of experiments twelve of the animals were used, and the same results were obtained. Here the electric bulb was slowly shifted in a circle around the dish, and the copepods slavishly followed the light. It is remarkable to note with what precision the organisms shift, when the position of the light is gradually changed. Time and time again, the animals made the complete round of the dish.

The definiteness with which the copepods orient to light is even more easily discerned when an oblong dish is used. Eight copepods were placed into a glass dish whose dimensions were eight inches long, one and one-fourth inches high, one and one-fourth inches wide, and were allowed to remain in the utter dark for about an hour. Then the current was switched on to a 60 c. p. Mazda globe, which was previously arranged in place at one end of the dish. The sudden flash caused the organisms to leave the bottom and to swim actively about in every direction. Shortly, however, they all made their way into the most highly illuminated region and remained there. Now a similar electric lamp, stationed at the opposite end of the dish, was turned on, while at the same time the first globe was extinguished. The copepods soon began to shift their position. One after another, they circled through the water, actively

making their way from the dark side of the dish to the lighted region. In two instances, the organisms were timed. In the first case it took the copepods five minutes to traverse the entire length of the dish, while in the second instance the time was six minutes.

3. *Behavior in light of low intensity.*—In light of low intensity, the copepod does not react quite as definitely as in strong light. This was brought out by the following experiment. An oblong glass dish was used, whose dimensions were the same as those of the oblong dish used in the previous experiment. Eight copepods were placed into it, and with a 60 c. p. Mazda lamp these were attracted to one end. Then the current was turned on to a 1 c. p. bulb stationed at the opposite end, while at the same time the other globe was extinguished. But the organisms paid little attention to the faint glimmer. Two or three of them were observed to travel a very short distance to the light, but no definite orientation occurred. When a 4 c. p. bulb was substituted for the 1 c. p. lamp, the same behavior resulted, no specific orientation taking place. If, however, an 11 c. p. globe was switched on, the animals oriented definitely, but slowly. They all moved to the illuminated side of the dish. A 16 c. p. bulb brought about this reaction more readily, and globes of higher intensity increased the positive behavior accordingly.

From these observations it becomes evident that the definiteness of orientation of the copepod varies with the intensity of illumination. Any increase in the illumination brings about a corresponding increase in precision of the specific reaction of the animal. Yerkes (1900), has noticed a similar behavior in Daphnia and Cypris.

The above experiments tend to bear out what was observed concerning the behavior of the copepods in their normal surroundings. While conducting hatching experiments it was noticed that whenever the covers of the hatching tanks were removed, the copepods would suddenly bob up to the surface of the water from underneath. This was observed many times and the regularity of its occurrence was very striking. The only explanation that could be found for this behavior was that the increase of illumination within the tanks attracted the animals to the surface. With this in mind, the foregoing series of light

experiments was undertaken. The results have convinced me of the fact that in ordinary daylight, especially in sunlight, the free swimming copepods move about close to the surface waters. In weak light, and in total darkness they sink passively to deeper regions.

The migrations of water dwelling organisms is a problem that has been studied by a number of investigators. Giesbrecht (1892), in his splendid report on the pelagic copepods of Naples, states that Weismann (1877), was the first one to attribute the upward and downward movement of pelagic organisms to the responses of these animals to light of different intensities. However, the first investigators to determine this question experimentally were Groom and Loeb (1891), who worked on the nauplii of the barnacle *Balanus perforatus*. In the laboratory, these investigators found that when the young were subjected to light of strong intensity, they reacted negatively, whereas in faint light, they were positive. These reactions were similar to the behavior of the nauplii in the open sea, where the larvae are found clinging to the surface of the water at night only, while during the day they swim about in deeper regions. Based on these observations, Groom and Loeb came to the following conclusion: "Das starke Licht bei Tage treibt die Tiere in die Tiefe, das schwache Licht, das auch in der Nacht vom Himmel ausgesandt wird, zwingt sie wieder in die Oberfläche emporzusteigen."

Loeb (1893) has brought forth additional evidence among marine copepods as well as other animals, such as Limulus and the Annelid Spirographis, which tends to strengthen the theory that light causes the periodic migrations of pelagic organisms. In this paper, however, Loeb calls attention to other factors besides light, such as gravity, which may also play an important part in determining these periodic movements.

Parker (1901), in his studies on the daily migrations of the marine copepod *Labidocera aestiva*, found that light was the most important factor in the vertical movements of these organisms. "*Labidocera aestiva* frequents the surface of the sea from sunset to sunrise. From sunrise to sunset, it is presumably in deeper waters. Its migrations are explained as follows: Females rise to the surface with the setting sun, because they are positively phototropic to faint light and negatively geotropic; they

descend into deep water with the rising of the sun, because they are negatively phototropic to strong light (their negative geotropism being overcome by their negative phototropism); the males follow the females in migration, because they are probably positively chemotropic toward the females."

Juday (1904), has studied the diurnal migrations of fresh water Plankton Crustacea, and found that most of these organisms come to the surface of the water at night, especially during the early part of the evening. Through most of the day, however, the animals occupied deeper water. He calls attention to the fact that diurnal movements are rather complex phenomena, and that they cannot be attributed to a single factor alone. Each lake presents different conditions, and these modify the behavior accordingly. The downward movement of the Plankton Crustacea he attributes to light, but he maintains that other factors, such as temperature, food, and the substances dissolved in the water may control the upward migrations of the animals.

Esterly (1907), working with Cyclops also emphasizes light as the directive agent in the migrations of this form.

It is thus seen that amongst marine as well as fresh water organisms we find a periodic migration. Light seems to play the most important factor in these movements. We must not, however, leave out of consideration such important factors as food, temperature and gravity, for these may also influence migrations, as was shown by Loeb (1893), Parker (1901) and Juday (1904).

In the case of Lernaeopoda we meet with an organism that offers an exception to the general rule of vertical migrations. Here we find the larva attracted by strong light, and it swims about close to the surface of the water during the day time, even overcoming its natural tendency to sink downward. At night, on the other hand, the animal does not react to weak light, and responds to the pull of gravity, thereby sinking to deeper regions. Clearly this behavior is of great value to the stability of the species. The migrations of the copepod are identical with the movements of its host. During the day trout generally feed near the upper surface of the water, whereas, at night they frequent lower regions.

VIII. REACTIONS TO HEAT

Loeb (1893), while experimenting with the copepod *Temora longicornis*, found that increasing the temperature of the water caused positively phototropic individuals to become negative, and vice versa; decreasing the temperature of the water brought about a change in normally negative individuals and caused them to become positive. Holmes (1901), found that increasing the temperature hastens, or may even induce, positive reactions among certain amphipods. This same author (1905), also found that an increase in temperature caused Ranatra to accentuate its positive phototaxis, while a decrease tended to produce the negative reaction. Yerkes (1900), could not induce any changes in the behavior of Daphnia and Cypris to light by varying the temperature. Parker (1901), also met with no success when he tried to induce changes in the light reactions of Labidocera by similar methods.

In the present experiments with heat, it was found that increasing the temperature of the water caused no change in the light reaction of Lernaeopoda. Six copepods were placed in an oblong dish of water, whose temperature was 58° F. These were then attracted to one end of the receptacle by a 60 c. p. Mazda lamp. At the opposite end, water that had been heated to near the boiling point was slowly poured at intervals a few minutes apart. As soon as the warmer water reached the animals they became very active, darting about rapidly; but none of them left the illumined side of the dish. As more hot water was supplied, the movements became slower, until at the temperature of 81° F. all of them were dead in the region of positive phototaxis. It was thus seen that increasing the temperature does not alter the behavior of the copepods to light.

IX. REACTIONS TO CHEMICALS

The effect of chemicals was next tried, with two purposes in view: first, to determine whether chemicals could reverse the behavior of the copepods to light, and second, to find out the solution of the chemical necessary to kill the parasitic organism while in this free-swimming stage of its existence. Only the first of these problems will be discussed here. The other will be dealt with in another paper on the economic aspects of *Lernaeopoda edwardsii*.

The chemical experiments were all performed at night, when the only source of illumination was a 60 c. p. Mazda globe stationed about a foot from the receptacle containing the copepods. Most of them were also confirmed in diffuse day-light. The observations were made in oblong glass dishes whose dimensions were eight inches long, one and one-fourth inch wide, and one and one-fourth inch high. The number of copepods used in each case was four or more.

Before applying a reagent, the copepods were first attracted to one end of the dish and then the chemical was slowly poured, drop by drop into the opposite end of the vessel. The following table gives a condensed statement of the results obtained. The sign + is used whenever the copepods reacted positively to light, whereas the sign — is used when the reaction to light was negative.

Chemical used	Lowest percentage of chemical causing death	Time required to kill copepod	Behavior to light until death
Sodium chloride	1.2	15 min.	+
Potassium chlorate.........	0.2	4 "	+
Calcium chloride...........	0.85	4 "	+
Hydrochloric acid..........	0.08	2 "	+
Sulphuric acid.............	0.015	3 "	+
Tartaric acid..............	0.45	2 "	+
Oxalic acid................	0.3	2 "	+
Copper sulphate...........	0.2	5 "	+
Acetic acid................	0.1	3 "	+ (indication of reversal)
Nitric acid................	0.03	16 "	+ (indication of reversal)
Magnesium sulphate........	1.6	45 "	2 +, 2 —
Hydrogen peroxide.........	9.0	18 "	—

Copper sulphate was found to affect the copepods differently during the day than at night. In the dark room a solution of 0.2 per cent copper sulphate caused all the copepods to die in about five minutes. In daylight, however, a two per cent solution of the chemical affected the animals very little. After remaining in this medium for twenty minutes they appeared to be as active at the end of this time as at the beginning. When the solution was increased to three per cent the organisms died in about four minutes. Evidently these differences in the behavior of the free swimming copepods depend upon differences in their physiological states, which may perhaps have been due to minute differences in the environment of the animals at the

times when they were secured; perhaps the individuals used during the day were younger, and therefore possessed greater vitality.

In acetic acid, nitric acid, magnesium sulphate and hydrogen peroxide the copepods gave indications of reversal in their behavior to light.

Acetic acid.—Acetic acid was slowly added until the water became a 0.1 per cent solution of the chemical. As the acid reached the copepods they became very active. One of them circled clear across the dish from the side nearest the light to the opposite end. The next moment, however, it moved into the light again, where it remained till death. In three minutes all of the. copepods died in the illuminated region.

Nitric acid.—This chemical was slowly added to a dish of water containing four copepods. When the medium became a 0.03 per cent solution, the animals became very active, darting rapidly about in the light for nearly ten minutes. Then two of them died, while the other two moved a little towards the opposite side. The latter reaction was but momentary, however, and the copepods again returned to the illuminated region. One now began to move away from the lighted side, but when it traveled about one-third the distance it returned into it again and remained there till death. No actual reversal took place although there were very strong indications of the organisms trying to avoid the chemical.

Magnesium sulphate.—These observations lasted from 8.22 P. M. to 9.10 P. M. When the magnesium sulphate was added to the water gradually, the copepods remained positive until the concentration reached one per cent. Here the addition of the chemical was suspended, and after a wait of a few moments, one copepod was seen making its way from the lighted region, while the others kept moving about within it. When a card was suddenly flashed between the dish and the light, the passing shadow caused the negative copepod immediately to become positive again. When more magnesium sulphate was added until the solution was 1.6 per cent, two copepods died, while the other two became negative. Passing a shadow between the light and the dish brought them back again into the positive region, but as soon as this ceased, they again became negative.

One persisted in remaining here, while the other copepod darted back into the lighted side of the dish. About three minutes later the organisms died.

The following evening this same experiment was repeated. When the concentration reached 1.7 per cent, two copepods became negative. One of these became positive again. The concentration of the solution was now increased until it reached a strength of four per cent, but the copepods behaved as before, one remaining negative, while the others were positive. Every now and then one of the positive three would dart away from the light, but the next moment it would again become positive. The copepods were not killed in this solution in thirty minutes. We thus meet a parallel with that noticed in the discussion of the reaction to copper sulphate,—a difference in the physiological state of the copepods.

Hydrogen peroxide.—This chemical caused a distinct reversal in the behavior of the animals to light. When the water became a nine per. cent solution of the chemical, all of the copepods, which up to this time had been darting about in the lighted region, suddenly reversed their direction and began to move away from the light. One died almost instantly, while the other three traveled about three-fourths the length of the dish. The motion of these copepods now became very slow; their dorsal muscles were affected to such a degree that the swimming feet could no longer beat with enough force to propel them through the water. The mouth appendages also stopped moving, and fifteen minutes later the copepods died.

From these results it becomes evident that the chemicals used have little effect on the behavior of the copepods to light. In a few cases a reversal in the orientation was observable. This was produced by the addition of hydrogen peroxide, magnesium sulphate, nitric and acetic acids. In the last three cases, however, the reversal may have only been incidental, for but one or two of the copepods became negative while the others remained positive. Generally those that did become negative remained in this region but a short while, and soon returned to the illuminated territory. In all the tests, when the chemical reached the animals they became very active, as if trying to get away from something that was affecting them severely. But as the concentration of the medium was grad-

ually increased, the motion of the copepods became slower, until death finally overtook them in the lighted side of the dish. The organisms are so strongly positive in their reaction to light, that they persist in going toward the source of greatest illumination, even though they are brought into regions that are dangerous to their existence.

X. INFECTION EXPERIMENTS

In the hatchery ponds, as well as in the natural streams *Lernaeopoda edwardsii* was found to attack the brook trout only. A great many rainbow trout as well as German-brown trout were examined and not a single case of infection by the copepod was observed. Furthermore, suckers that were kept in the hatchery ponds, as well as those thriving in neighboring trout streams were examined, but were found to be clean and healthy. Now the question arose: What explanation could be offered for this choice on the part of the copepod for the brook trout only? In attempting to determine this a series of infection experiments were undertaken.

Three groups of three copepods were placed into three separate dishes of water. Into each dish was then placed, respectively, the gills of freshly killed brook, rainbow and German-brown trout. The fresh blood of the gills soon began to diffuse in the water and the behavior of the copepods was noticed. The copepods in the first dish into which the gill of the brook trout was thrown, became very active, darting about in every direction, as if they were in search of something. In the other two dishes, which contained the gills of the rainbow and German-brown trout, no such reactions of the copepods were noticeable. Two of the animals came in contact with the brook trout gill and began to attach themselves. In the other two dishes no attachment took place, in spite of the fact that the organisms came in contact with the gills a number of times.

The manner in which the copepod attaches itself to the gills of the brook trout is very interesting. Wilson (1911), in his paper on the development of *Achtheres amblophitis* Kellicott, a copepod of the family Lernaeopodidae, parasitic on the gills of the rock bass, describes the attachment of the organism as follows: "Of course, it is practically impossible to actually witness the fastening of the larva. But what has been observed

in the chalimus larva of the Caligidae, we can infer what occurs
here. The outer end of the attachment filament is enlarged
into the mushroom form already described, and is filled with
adhesive fluid. It lies just inside the frontal margin, covered
only by a very thin outer cuticle. Doubtless, the larva rubs
its frontal margin against the skin of the gill arch of its host
and in this way burrows through the slime and outer integu-
ment to the solid tissue underneath, holding on meanwhile
with its powerful maxillipeds. At the same time the thin
covering of the frontal margin of the parasite is broken through
and the end of the filament is brought in contact with the gill
arch, to which it adheres firmly. By moving away from the
point of attachment the coiled filament is drawn out of the
body of the larva. As it comes forth the larva grasps it between
the claws at the tip of the second maxillae."

This process of attachment as surmised by Wilson, however,
was not found to be the method by which *Lernaeopoda edwardsii*
attaches itself to the gills of the brook trout. By the aid of
the microscope I observed the process of attachment four times.
As soon as the copepod comes in contact with the filament of
the gill, its mouth parts are inserted into the flesh, and by means
of the powerful claw-like second maxillae it begins to rasp the
filament until it forms a cavity within it. As soon as this occurs,
the anterior portion of the copepod's head, the frontal margin,
is brought in contact with the cavity and the enclosed attach-
ment filament is injected into the hole. The spherical mush-
room body adheres to the flesh and the regenerating tissue of
the gill soon encloses it tightly, thereby fastening the organism
firmly. The mouth parts are then withdrawn from the flesh of
the gill filament. In this condition the parasite remains attached
for a short time. Then the second maxillae detach the posterior
region of the attachment filament from the head margin and
they themselves become permanently attached to this end of
the filament. Degeneration soon sets in and the organism
changes considerably. The female copepod remains thus attached
throughout life, while the male remains attached in this way
until shortly before it is mature for copulation.

Wilson believes that the transference of the filament from the
frontal margin to the tips of the second maxillae takes place
at the time of fixation to the host, and that the larvae are never
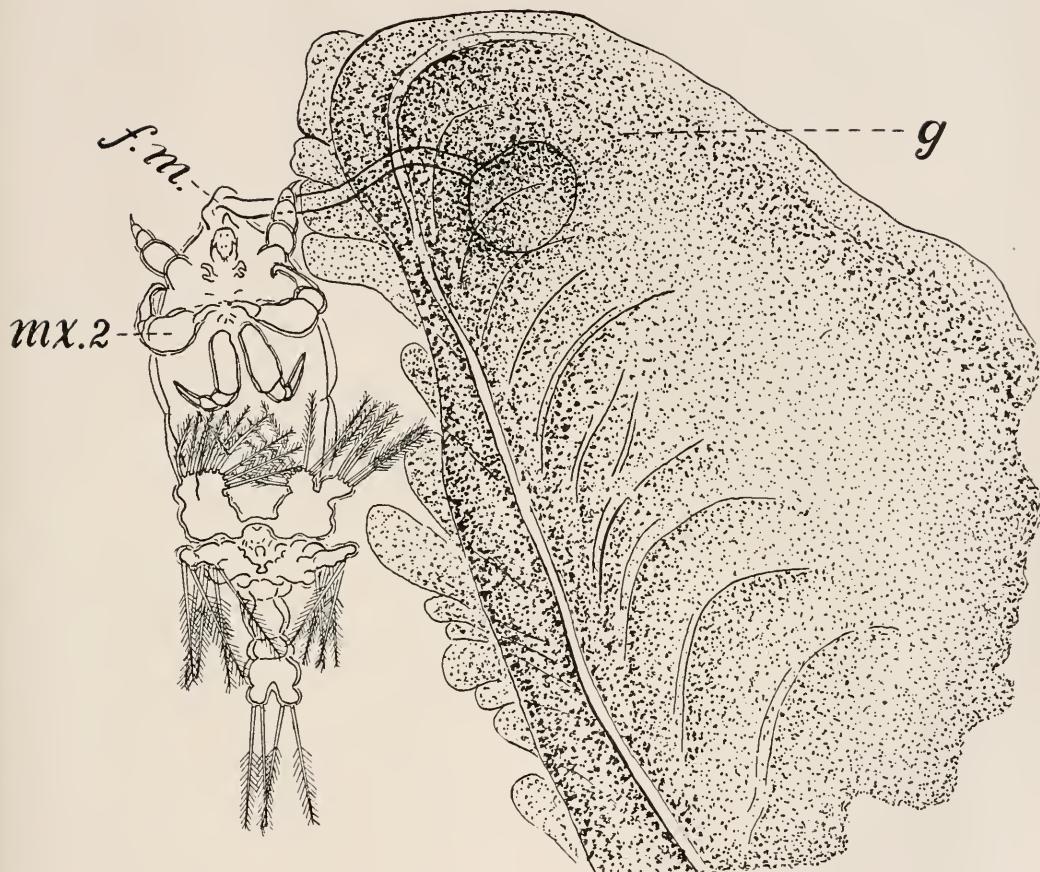
FIGURE 6. Lernaeopoda edwardsii. Larva attached by frontal margin, x 110
f. m. =frontal margin.
g. =gill.
mx. 2=second maxilla.

found fastened by their frontal margins. Figure 6 is a camera lucida drawing of a larva of *Lernaeopoda edwardsii* thus attached.

Let us now come back to the infection of the fish. In order to study the problem further, a floating cage was sunk in one of the hatching tanks, and into it were placed healthy specimens of brook trout, rainbow trout and perch. The fish were examined two days after the sinking of the cage and the brook trout were found to be the only species infected; the others were all

clean. Five days later the perch died, but their gills revealed no infection by Lernaeopoda, their death was apparently due to a fungus which had developed on them. The rainbow trout were also found to be free from the copepod.

Lefevre and Curtis (1912), in their recent paper on the artificial propagation of fresh water mussels, note a similar preference on the part of the hookless glochidia of the genus Lampsilis for certain fishes. However, they have found that the glochidia may attach themselves to a number of different kinds of fish, although their choice for one is generally predominant. The glochidia are therefore not quite as exclusive in their choice as are the free swimming Lernaeopoda. The reactions observed in the glochidia and in the copepod are, undoubtedly, chemical in nature. In the case of the copepod there must be something in the blood or other secretions of the brook trout which attracts the parasite to this species of fish. This chemical substance, or substances, must be wanting in the other fish and they are, therefore, not parasitized by *Lernaeopoda edwardsii*.

XI. CONCLUSIONS

From the foregoing discussion it becomes evident that *Lernaeopoda edwardsii* is well adapted to its parasitic mode of life. It moves about with a darting spiral motion, thereby covering a maximum of territory with the amount of energy it expends. In many respects this method of locomotion is similar to that of the hunter ciliates. The organism is so strongly attracted by intense light that during the day it frequents the upper regions of the water, though it is normally positively geotropic. In this position the copepod is very favorably situated, for the brook trout feed near the surface waters throughout most of the day, and hence the parasite is readily accessible to them. At night, on the other hand, the copepods are no longer attracted by light, and since they possess a greater specific gravity than the water, they passively sink to deeper regions. Here, also, their position is advantageous because after sunset the trout frequent the lower strata of water, and they are thus stationed close to the parasites where infection may occur and the life of the copepod thus insured.

XII. SUMMARY

1. *Lernaeopoda edwardsii* is a parasitic copepod which attaches itself to the gills of the brook trout. It attacks this species of trout only, the rainbow as well as the German-brown trout being immune from it. Undoubtedly, its reaction to the brook trout is a chemotactic one.

2. The free-swimming existence of the organism is very short, about two days at the most, and during this stage of its life history it swims about with a darting spiral motion.

3. When the copepod stops moving through the water, it sinks to the bottom in an upright position, with its head down. When it strikes bottom it may rest either on its ventral or dorsal side, depending entirely on which side of the animal strikes the bottom first. Undoubtedly the organism sinks because its specific gravity is greater than that of water.

4. Lernaeopoda is strongly positive in its reactions to intense light. In light of low intensity, however, it is indifferent. Because of its affinity for strong light, the copepod moves about near the surface of the water during most of the day. At night, the animal remains indifferent to weak light, and through its specific gravity it sinks to deeper waters.

5. Increasing the temperature of the water does not change the behavior of the organism to light.

6. Some chemicals have little effect on the behavior of *Lernaepodao edwardsii* to light. No reversal in the positive behavior of the larva could be induced through the use of sodium chloride, potassium chlorate, copper sulphate, calcium chloride, hydrochloric, sulphuric, tartaric and oxalic acids. In hydrogen peroxide, magnesium sulphate, nitric and acetic acids indications of reversal were noticeable.

XIII. BIBLIOGRAPHY

BATESON, W. Notes on the Senses and Habits of Some Crustacea. Jour. Mar.
1887. Biol. Assoc. United Kingdom, vol. 1, p. 211.

BINET, A. The Psychic Life of Micro-Organisms. The Open Court Publishing
1903. Co., Chicago. 120 pp.

ESTERLY, C. O. Reactions of Cyclops to Light and to Gravity. Amer Jour.
1907. Physiol., vol. 18, pp. 47-57.

GIESBRECHT, W. "Systematik und Faunistik der Pelagischen Copepodendes
1892. Golfes von Neapel und der Angrenzenden Meeres-Abschnitte."
Fauna und Flora des Golfes von Neapel—XIX, Monogr., pp. 806-809.

GROOM, T. T., und LOEB, J. Der Heliotropism der Nauplien von Balanus perfo-
1891. ratus, und die periodischen Tiefwanderungen pelagischer Tiere.
Biologisches Centralblatt, Bd. X, pp. 160-177.

HOLMES, S. J. Phototaxis in Amphipoda. Amer. Jour. Physiol., vol. 5, pp. 211-
1901. 234.
1905. The Reactions of Ranatra to Light. Jour. Comp. Neur. and Psych.,
vol. 15, pp. 305-349.
1912. The Evolution of Animal Intelligence. Henry Holt & Co. New York.
296 pp.

JENNINGS, H. S. On the Significance of the Spiral Swimming of Organisms. Amer.
1901. Naturalist, vol. XXXV, no. 413, May, pp. 369-378.
1904. Contributions to the Study of Lower Organisms. Carnegie Inst. of
Washington, pub. no. 16, 256 pp.
1906. Behavior of Lower Organisms. Macmillan & Co. New York. 366 pp.

JUDAY, C. The Diurnal Movement of Plankton Crustacea. Trans. Wis. Acad.
1904. Sci., Arts & Letters, vol. XIV, pp. 534-568.

LEFEVRE, G. and CURTIS, W. C. Studies on the Reproduction and Artificial Pro-
1912. pagation of Fresh Water Mussels. Bull. U. S. Bur. Fisheries, vol.
XXX, 1910, pp. 105-201.

LOEB, J. Ueber kunstliche Umwandlung positiv heliotropischer Thiere in negativ
1893. heliotropische und umgekehrt. Arch. f. d. ges. Physiol., Bd. 54,
pp. 81-107.
1894. On the Influence of Light on the Periodical Depth Migrations of Pelagic
Animals. Bull. U. S. Bur. Fisheries for 1893, pp. 65-68.
1904. The Control of Heliotropic Reactions in Fresh Water Crustaceans by
Chemicals, Especially CO_2. The Univ. of Cal. Publ. Physiol., vol.
2, no. 1, pp. 1-3.
1906. The Dynamics of Living Matter. The Macmillan Co. 233 pp.

MAST, S. O. The Reactions of Didinium nasutum (Stein), with Special Reference
1909. to the Feeding Habits and the Function of the Trichocysts. Biol.
Bull., vol. 16, pp. 91-118.
1911. Light and the Behavior of Organisms. John Wiley & Sons, New York.
410 pp.

PARKER, G. H. The Reactions of Copepods to Various Stimuli and the Bearing
1902. of this on Daily Depth Migrations. Bul. U. S. Bureau of Fisheries
for 1901, pp. 103-123.

SCOURFIELD, D. J. The Locomotion of Microscopic Aquatic Organisms. Jour.
1909. Q. Micros. Club, vol 10, no. 64, pp. 357-366.

TOWLE, E. W. A Study in the Heliotropism of Cypridopsis. Amer. Jour. Physiol.,
1900. vol. III., pp. 345-365.

WHITMAN, C. O. Animal Behavior. M. B. L. Lect., Woods Hole, Mass., pp. 285-
1898. 338.

WILSON, C. B. North American Parasitic Copepods Belonging to the Family
1905. Caligidae. Proc. U. S. Nat. Mus., vol. 28, pp. 479-672.
1911. North American Parasitic Copepods. Part 9—The Lernaeopodidae.
Proc. U. S. Nat. Mus., vol. 39, pp. 189-226.

YERKES, R. M. Reactions of Entomostraca to Stimulation by Light. II. Reac-
1900. tions of Daphnia and Cypris. Amer. Jour. Physiol., vol. IV, pp.
405-422.

THE REACTIONS OF CERTAIN DERMESTIDAE TO LIGHT IN DIFFERENT PERIODS OF THEIR LIFE HISTORY

J. E. WODSEDALEK

The Zoölogical Laboratory, The University of Wisconsin

PHOTOTACTIC REACTIONS OF *TROGODERMA TARSALE*, A MUSEUM PEST

While working on the life history and habits of T. tarsale[1] I made some observations which suggested the idea that it would be an advantage to know the exact phototactic reactions of this beetle in the different periods of its life history. Careful observations were made and it was noticed that the larvae immediately after hatching evince a markedly negative reaction to light by concealing themselves in any available shaded areas. If placed near a window they at once begin to crawl away from the light, and the reaction is even more pronounced when the specimens are taken into a dark room and a strong light is introduced at one end of the glass dish containing them. This negative response persists throughout their larval life. Before passing into the pupal stage their negative reaction is especially pronounced. Thus, the pupae are almost invariably found in dark places which afford them a favorable means of protection.

After metamorphosis, the adults, both male and female, retain the negative phototaxis. As a rule the insects remain for some time within the feeding material or cabinet in which they were reared. A large number of newly emerged adults were taken into a dark room and both sexes manifested a decidedly negative response to light of various intensities. During the sexual excitement which follows a day or two later they still remain negative. The female remains markedly so until her eggs are safely deposited. Several hours later, or the day following the egg-laying, the negative reaction is gradually inhibited until the

---

[1] Wodsedalek, J. E. "Life History and Habits of Trogoderma Tarsale, a Museum Pest." Annals of the Entomological Society of America, vol. 5, No. 4.

insect becomes quite indifferent, and finally decidedly positive
even to intense light. The males, too, during the last days of
their lives become indifferent to light and often even strongly
positive in their phototaxis.

Although ordinarily the adults remain till death occurs in
the cabinets where they had developed, not infrequently do
we find some of them on the windows in the rooms where they
make their abode. A number of such specimens were at differ-
ent times collected and dissected, but in no cases were there
any eggs found within the bodies of the females. This also
indicates that they lay their eggs before they become posi-
tively phototactic and desert their places of concealment, and
apparently their destruction at this time is futile.

PHOTOTAXIS IN THE CARPET BEETLE OR "BUFFALO MOTH" (*ANTHRENUS SCROPHULARIAE*), AND ITS ECONOMIC IMPORTANCE

In view of the results obtained through the observations
and experiments on light reactions in T. tarsale, an idea sug-
gested itself that the light reactions in other Dermestidae might
be worked out to some economic advantage. The popular
belief in the case of the common carpet beetles is that the pests
metamorphose in the houses and immediately go outside to
breed, where they are often very abundant on flowers, and
that after this is accomplished the females return to the houses
to lay their eggs. Careful observations and experimental work
with this species, however, revealed facts contrary to the com-
mon belief.

In the spring of 1911 about six hundred adult specimens
were collected from the blossoms of Spiraea on the University
of Wisconsin campus. More than a hundred of the female
individuals were killed and dissected, but no eggs were found
within their bodies. The remaining insects were kept in the
laboratory with an ample supply of food with the view of ob-
taining some eggs. The jars containing the beetles were care-
fully examined but no eggs were secured. After the specimens
had all died, the jars were put in a convenient place with the
idea that possibly some eggs had escaped the writer's notice
and that in time some young larvae would probably appear;
but not a single individual was obtained.

A similar process was repeated in the spring of 1912. This time, however, the beetles were not as numerous on the flowers of Spiraea as they were the previous season, a fact probably due to the cool, rainy weather. About sixty female insects were dissected and over two hundred specimens of both sexes were kept alive for further observations. Again no eggs were procured. Not a single case of copulation was observed during the process of collecting about a thousand individuals in the two successive seasons. In the laboratory where the collected beetles were kept with an abundance of food and where most of them lived from five to fifteen days, again no evidence of sexual excitement was observed.

The same season I succeeded in getting a number of almost full grown larvae and also a number which were about half grown. The large specimens pupated and metamorphosed the first part of June and produced a new generation, the larvae of which were kept for further experimentation. The smaller larvae matured and reproduced in fall.

Experiments on light reactions were performed and, as in the case of T. tarsale, it was found that A. scrophulariae larvae are decidedly negative to light in all stages of their larval history. Also both sexes of this species manifested a decidedly negative reaction to light immediately after their emergence from the pupal skins. This response persisted through the period of fertilization and egg-laying. Very shortly after laying their eggs the female insects reversed their reaction to light, becoming decidedly positive. The males, too, completely reversed their phototaxis during the latter part of their lives. When the beetles were placed near a window they made frantic efforts to get outside. The same reversal was observed in experiments with an electric light in the dark room. Similar results were obtained with the specimens of the second annual generation which metamorphosed in fall.

L. O. Howard,[1] in his paper on the Carpet Beetle or "Buffalo Moth," says that it is probable that the migration of this beetle from the house takes place, under ordinary circumstances, after the eggs have been laid. The foregoing facts show conclusively

[1] Howard, L. O. The Carpet Beetle or "Buffalo Moth" (Anthrenus scrophulariae). Circular no. 5, revised edition, U. S. Dept. of Agric., Bureau of Entomology. This circular suggests some remedies for the checking of the pest which may also be applied to T. tarsale.

that the Carpet Beetles lay their eggs before they desert the houses. When their phototaxis is reversed they are attracted to the windows by the light and make their escape if possible. When they reach the open air they are attracted by certain flowers, particularly of the family Serophulariaceae. The blossoms of Spiraea on which they may be found by the thousands here in Madison, are also strongly attractive to the beetles. It is very probable that they spend the remainder of their lives on the blossoms, never returning to the houses. At any rate, they are harmless at this stage and if eradication would be effected they must be destroyed before they lay their eggs.

THE BLACK CARPET BEETLE (*ATTAGENUS PICEUS*)

The black carpet beetle, another of the Dermestidae, possesses habits somewhat similar to those of A. serophulariae and T. tarsale. Observations and experimental work on this species seem to indicate that it behaves practically the same in its phototactic reactions as do the other two beetles mentioned. However, I have been able to secure only a small number of specimens of this species and the results obtained, therefore, are not entirely conclusive as in the case of T. tarsale and A. serophulariae, both of which were obtainable in large numbers.
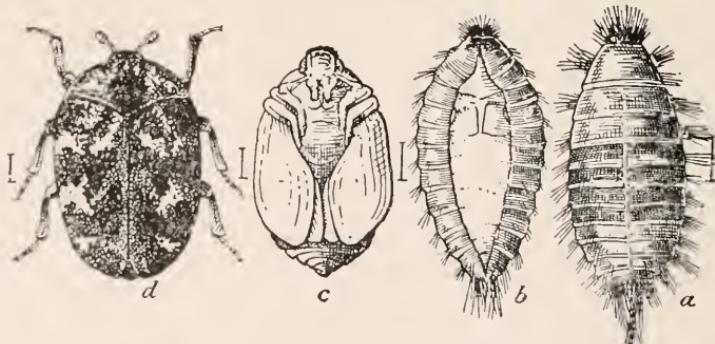
FIGURE 1. The carpet beetle (*Anthrenus scrophulariae*): *a*, larva, dorsal view; *b*, pupa within larval skin; *c*, pupa, ventral view; *d*, adult. All enlarged (from Riley).

SIZE AND FORM PERCEPTION IN
GALLUS DOMESTICUS

HAROLD C. BINGHAM
Ellsworth College
From the Harvard Psychological Laboratory

Four figures

CONTENTS

I. APPARATUS

A frequent defect appearing in past experiments on visual acuity in animals is the inadequate description of methods. In many cases the conditions have been such that they could not be accurately described. Complexities have been involved making it impossible to ascertain with certainty the visual factors on which the animals have relied in their discriminations. The apparatus used in the observations which are reported in this paper was devised for the purpose of overcoming this difficulty. Controllability was the primary aim in its construction.

To Professor Yerkes, under whom this study was made and
to whom I am indebted for assistance and suggestions, credit
is due for many of the points of method here described.   A
report has been published by him and Professor Watson [1] in
which the details of parts of the apparatus have been presented.
For the detail of divisions *2* and *3* the reader is referred to the
Yerkes and Watson report.   In order to give a comprehensive
idea of the mechanism, I shall describe the complete apparatus
as it appeared during my work, abbreviating, as much as possible,
descriptions of the parts which have been previously described.

Figure 1 is an isometric view of the apparatus as a whole
showing only the skeleton of the different parts when assembled
for experimental work.   I shall speak of that part of the mechan-
ism labelled I as the *experiment box*.   The opposite end, III, is
the light or *source box*.   Between the experiment box and the
source box is a *stimulus shifter*, II.   The whole apparatus was
set up in a dark room.   The only sources of illumination were
the lamps in the source box and a lamp, L, hanging directly
above the experiment box.   With these sources cut off, a dark
adapted human eye could see slightly, for a few small cracks
in the room allowed faint rays of light to enter; but the sub-
sequent description will show that these factors were of no
consequence.

As a means of testing the chicks' ability to discriminate
between sizes and forms, two illuminated areas differing from
each other with respect to one or both of these factors are simul-
taneously exposed before the experiment box, I.   The problem
for the animal is to learn regularly to choose one of these stimuli
and to reject the other.   It is punished by means of an electric
shock for a wrong choice and is rewarded for a right choice
by escape to a warm, dry nest box where food, light, water,
and companionship are to be found.   The illumination of the
visual stimuli comes from the source box, III, which is con-
structed so that the brightness of either stimulus area may be
independently controlled.   The light is admitted to two of
three regulated apertures in the shifter, II, the function of
which is to facilitate changes in the size, form, or relative posi-
tion of the stimulus areas.

---

[1] Yerkes, Robert M. and Watson, John B.   Methods of studying vision in ani-
mals.   *Behavior Monographs*, 1911, vol. 1, no. 2, S. N. 2.
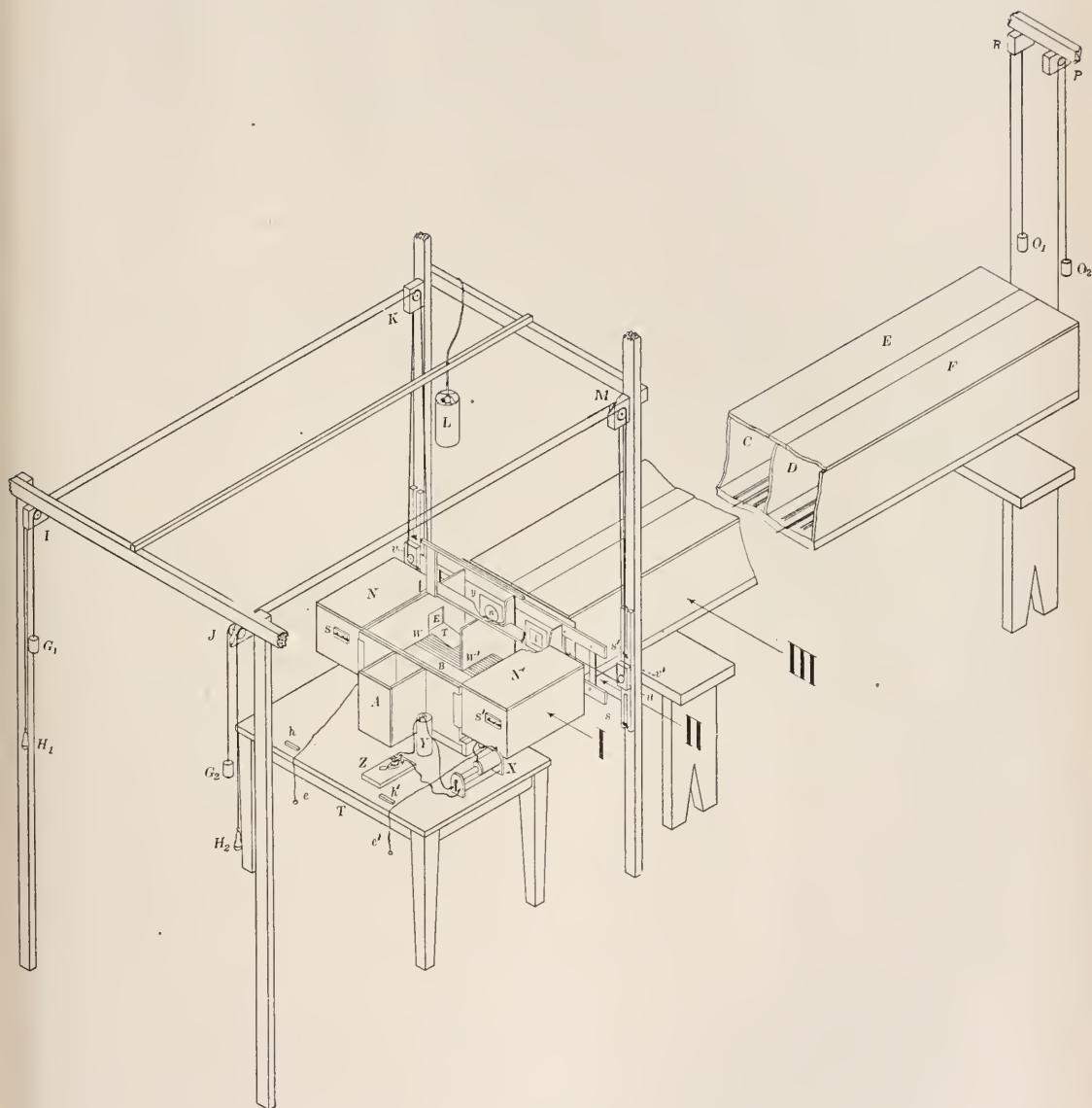
FIGURE 1.   Isometric view of *light* vision apparatus.

If the form of the two end stimulus areas is square, and that of the middle one is circular, a movement of the adapter to the left produces the condition shown in figure 1. The stimulus *l*, at the right is a square and that, *n*, at the left is a circle. But when the shifter is moved to the right and the relative positions of the two forms with respect to each other become reversed since the square at the extreme left (now invisible) will take the place of the circle, the circle will move over to the place now occupied by the square, while the present square will be shifted to the extreme right and will become invisible.

This brief account of the apparatus as a whole should make it possible to grasp more easily the details of the various sections. An understanding of the construction and use of the mechanism will be made less difficult if the details are now considered in connection with each general part.

1. *Experiment box*

An illustration of the experiment box appears as figure 2. This section of the apparatus is made of one-half inch lumber, (except where stated otherwise), and is painted within and without a dead black. It consists of four main parts: (1) A is an entrance chamber, $15\frac{1}{2}$ x 20 x 22.[2] The floor of A is provided with a metal tray containing a piece of wet felt which fits the floor of the chamber. The entrance box may be removed by raising out of the iron straps, C and C', the board to which it is attached. (2) B is a discrimination chamber, 26 x 51 x 22. Leading from A to B is an entrance, I, 8 x 10. The floor of B, like that of A, is carpeted with wet felt. The tray of either compartment can be easily removed and cleaned. (3) W and W' are electric boxes separated from each other by the partition D. On the floors of W and W' are fitted pieces of slate, $16\frac{1}{2}$ x $24\frac{3}{4}$ x 1, carrying electric wires by means of which an animal can be shocked when its behavior demands punishment. By means of the interposited sides, O O O, the electric compartments are set back 14 cm. from the stimulus shifter. The floor of this extended portion drops down about 10 cm. below that of W-W'. The middle O stands up closely to the adapter so that the exposed stimuli are set off from each

---

[2] Unless otherwise stated, dimensions are given in centimeters and the order of presentation is length, width, and depth—inside measurements.

other. On the end of DO is glued a piece of piano felt, P, which rubs snugly against the shifter and prevents any intermingling of the stimulus illuminations, while at the same time, the shifter can be freely moved in either direction without becoming scratched or marred by the friction. (4) N and N' are nest boxes, $40\frac{1}{2}$ x 22 x 22. Each nest box is covered by a tightly
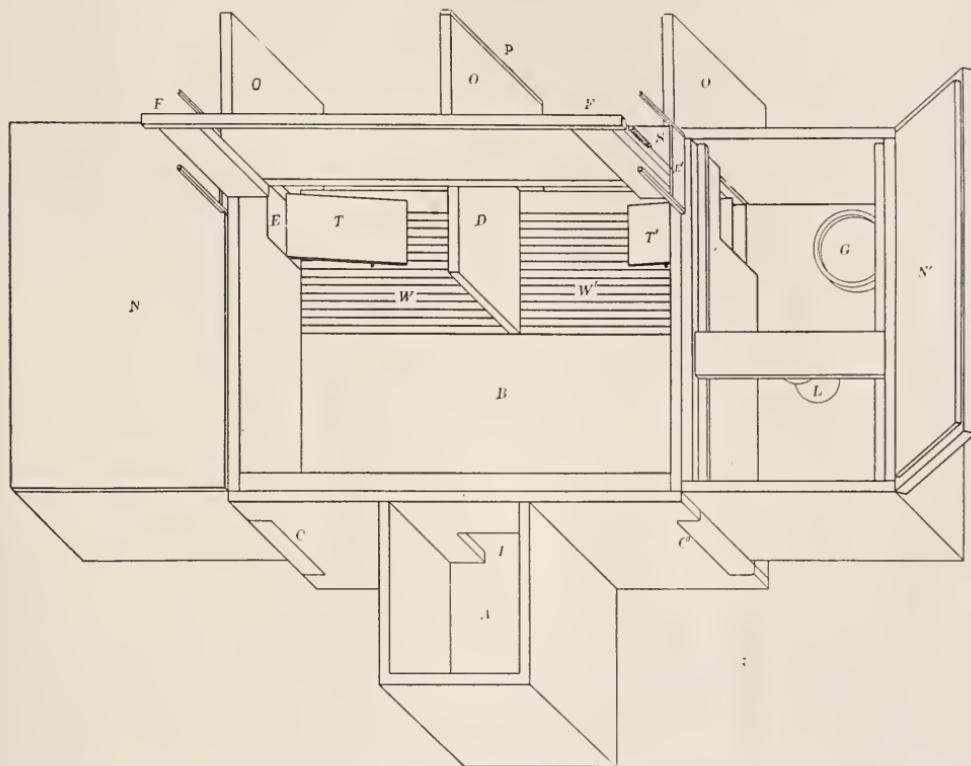
FIGURE 2. Experiment box

fitting lid, which is hinged at the outside, and is equipped with a 2 c.p. electric lamp (frosted globe), L, a watch glass for water, G, and sand or litter in which food may be scattered. It is also provided on the outer side with hidden holes for ventilation.

Between W and N, also W' and N', is a vertically sliding door, E closed and E' open, 3 mm. thick which fills an opening 8 x 10. Suspended from an upright frame, F, is a coiled spring, S, which passes through the walls of N' and B-W' to the top

of E. When E is closed S is extended and in a state of torsion, hence when E is released S tends to return to a state of rest and the doorway is opened. The method of closing the doorway may best be seen in figure 1. A silk line, e, which passes up through a wire loop directly under E is attached to the
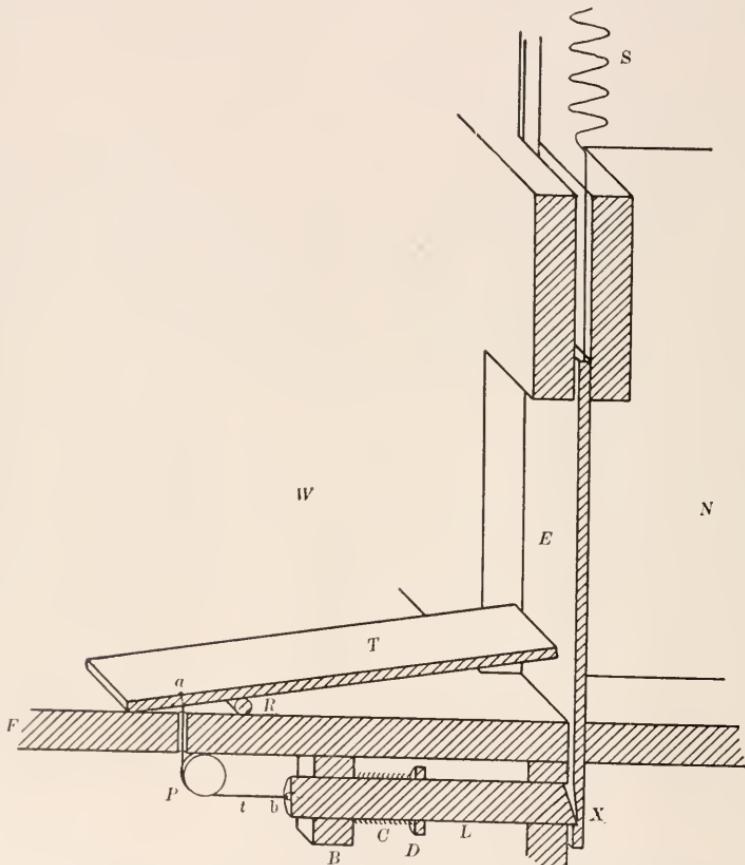
FIGURE 3. Automatic tripping device of the experiment box.

lower part of the door. By pulling on e the experimenter can close E which automatically locks when it is closed. By stepping on or striking T the chick can release the lock. The experimenter, however, by catching e on the hook h can prevent the door from opening when the T-lock has been released. This automatic release was devised by Professor F. S. Breed.

The construction of this mechanical device for opening E appears in figure 3 of which T is the trip that was seen in the other figures and *t* is a short piece of No. 30 black thread attached to T at *a*. Passing down through the floor, F, of the electric box, W, *t* runs over a pulley, P, and is fastened to the spring lock, L, at *b*. B is a block through which L passes and against which one end of the spring, C, presses. D is a stop attached to L supporting the other end of C. This spring tends to force L in the direction of X and to keep T in the position as illustrated. But when sufficient pressure is applied to T at any point above R, L is forced back in spite of the pressure of C, E is released at X, and the recoil of S raises E. When E is drawn down, L, by reason of the slanting end surface at X, is forced toward P until the notch of E has passed below the lower side of L when the constant pressure of C toward X forces L into the notch of E and the door is again locked.

In several respects figure 3 is a very poor representation of the tripping device. L is shown as constructed solidly in B, when, in reality, it slides very freely through B. Moreover, L is sadly disproportioned for it appears in the figure as wide as the floor of the experiment box, but it is really a delicate latch narrower than the width of T or E and is released by a very light touch upon T.

2. *Source box*

To provide illumination for the two stimuli simultaneously presented to the chick, the source box represented in figure 4, —III of figure 1,—was used. A complete description of this part of the mechanism appears in Behavior Monographs, *loc. cit.*, p. 17*ff*.

3. *Stimulus shifter*

Figure 4 also presents a general view of the stimulus shifter by means of which size, form, position, and, in conjunction with the lamp carriages, brightness of the visual stimuli can be regulated. The details of the stimulus shifter or adapter appear in the Yerkes and Watson report.

A considerable number of standard brass stimulus plates, used for varying the size and form of the visual stimulus, is required if an animal's discriminative ability is to be deter-
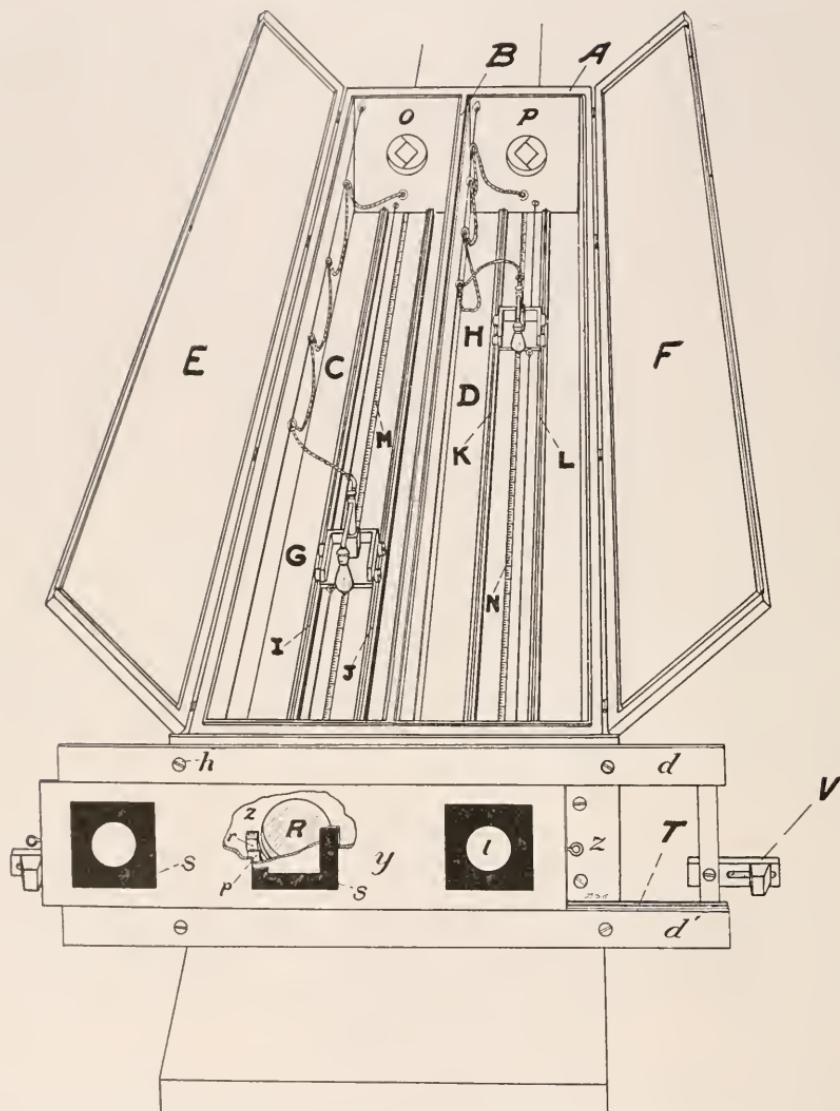
FIGURE 4. (Reprinted from *Behavior Monographs*, 1911, vol. 1, no. 2, p. 18.)
" Perspective of *light* or 'brightness' apparatus.   A, light box; C, D, com-
partments of A; B, partition between C and D; E, F, lids of A; G, H, metal
carriages carrying tungsten lamps; IJ and KL, tracks for G and H; M,
N, Starrett steel millimeter tapes; O, P, apertures covered by Aubert dia-
phragms; R, Bausch and Lomb cooling cell in light box; d, d′, metal straps;
y, aluminum plate sliding between d and d′; T, tracks for y; V, stop for y;
z, steel plate bolted to wooden end of light box; h, screws attaching y to
z; s, s, standard brass stimulus plates; p, brass frame about aperture in y;
r, hard rubber ring screwed to p."

mined. Part of the set I used, which consisted of 47 plates, is included in table 1. Owing to the variations in sensitiveness among different subjects, a set which would meet the requirements for one animal would not suffice for another, hence, in those cases where the size differences among the plates vary by one millimeter, a safe margin has been allowed by enumerating a few more plates than would ordinarily be required, and those plates for which I found no use have been omitted.

4. Accessories

Connected with both ends of the stimulus shifter, II, figure 1, page 67, are two ropes which pass over several pulleys and terminate at H_1 and H_2. These ropes hang 85 cm. back of the table, T, thus leaving the experimenter an abundance of free space at the front of the apparatus. They are separated from each other by 110 cm. The purpose of this attachment is to enable the experimenter to change the position of the shifter without leaving his place of observation. As is shown in the initial figure, the shifter can be moved from its present position to the right side by pulling on H_2. H_1 would thus be raised, and by pulling on it the adapter would be returned to its present position. The stops v and v' are so adjusted to the shifter that the openings in the brass plates will fall directly in the line of illumination from the source box. These stops are horizontally adjustable (not shown in the figure). The center of the pulley which v carries is $92\frac{1}{2}$ cm. above the floor. The pulleys at I, J, K, and M are 230 cm. from the floor. The distance from I to K and from J to M is 200 cm.

Arranged upon the same frame is another system of ropes and pulleys devised to control the positions of the source lamps. The terminals of these ropes are indicated by G_1 and G_2 at the experiment end, and by O_1 and O_2 at the opposite end. The drawing accurately represents the actual conditions at the experiment end, but on account of the arrangement of the walls of the dark room, O_1, O_2, R, and P merely represent the principle of the system. The ropes G_1-O_1 and G_2-O_2 are centrally attached to the source carriages of C and D. By lifting slightly upon G_1, O_1 begins to lower and draws back the lamp carriage through C. By lightly pulling down upon G_1, the carriage in C is drawn forward. The system G_2-O_2 works similarly.

TABLE 1
Stimulus Plates

Use	Form	Diameter or Side	Area	Number Plates Needed
To test Size Perception	Circle	cm. 1.8	sq. cm. 2.5447	1
"	"	1.9	2.8353	1
"	"	2.0	3.1416	1
"	"	2.1	3.4636	1
"	"	2.2	3.8013	1
"	"	2.3	4.1548	1
"	"	2.4	4.5239	1
"	"	2.5	4.9088	1
"	"	3.0 (standard)	7.0686	2
"	"	3.5	9.6211	1
"	"	4.0	12.5664	1
"	"	4.1	13.2026	1
"	"	4.2	13.8545	1
"	"	4.3	14.5220	1
"	"	4.4	15.2053	1
"	"	4.5	15.9043	1
"	"	4.6	16.6191	1
"	"	4.7	17.3495	1
"	"	4.8	18.0956	1
"	"	4.9	18.8575	1
"	"	5.0	19.6350	1
"	"	5.5	23.7583	1
"	"	6.0 (standard)	28.2744	2
"	"	6.1	29.2247	1
"	"	6.2	30.1908	1
"	"	6.3	31.1725	1
"	"	6.4	32.1700	1
"	"	6.5	33.1832	1
"	"	6.6	34.2120	1
"	"	6.7	35.2566	1
"	"	6.8	36.3169	1
"	"	6.9	37.3929	1
"	"	7.0	38.4846	1
"	"	7.1	39.5920	1
"	"	7.2	40.7151	1
"	"	7.3	41.8540	1
"	"	7.4	43.0085	1
"	"	7.5	44.1787	1
"	"	8.0	50.2656	1
"	"	8.5	56.7455	1
"	"	9.0 (standard)	63.6174	2
				44
To test Form Perception	Circle	cm. 6.0 (as above)	sq. cm. 28.2744	–
"	"	5.9	27.3397	1
"	"	5.8	26.4208	1
"	"	5.7	25.5176	1
"	"	5.6 and smaller circles used in size perception	24.6301	1
"	Square	5.317 (side)	28.2743	2
"	Equilateral △	8.081 (side)	28.2743	2
		Openings inscribed in circle—28.2744		
"	Square	4.243 (side)	18.003	2
"	Equilateral △	5.196 (side)	11.691	2
				12
				Total 56

The experimenter is thus enabled to control the intensities of the stimulus areas without leaving his end of the apparatus. By moving a carriage backward the intensity of the corresponding stimulus display is decreased; by drawing the source nearer, the intensity is increased.

Figure 1 also shows arranged on a table, T, the electrical connections with the experiment box. X, Y, and Z are respectively an inductorium, a Columbia dry cell (No. 6), and a telegraph key which, in connection with the wired slate floors of W and W', constitute an interrupted circuit. The wires are wrapped alternately about the slate floors so that by closing the key, Z, a chick, when its feet touch any two of the wires, can be shocked. With young chicks under two weeks of age it was found necessary in general to set the secondary coil at 5, but as they become older and heavier the strength of the shock had to be decreased, until, in some cases, the position of the secondary coil was as far out as 6.5. The letters s and s' indicate electric switches by means of which the illumination in N and N' can be turned on or off. An upper illumination, L, designed to hide inequalities in the distribution of light in each compartment, W and W', hangs about 120 cm. above the floor and directly over the center of the electric boxes. It consists of a 2 c.p. electric lamp inclosed in a vertically suspended cylinder of galvanized iron. The diameter of this cylinder is 10 cm. and its length is 20 cm. The upper end is closed. The lower end is fitted with a cover (like that of a baking powder can) which may be pushed on or off. Centered in this cover is an Aubert diaphragm by means of which the amount of light falling on the experiment box may be regulated. On account of the low ceiling of the dark room where these experiments were conducted, I found it impracticable to use the diaphragm. Unless it can be raised to a sufficient height it will cast shadows upon the floor of the experiment box. With the diaphragm removed, the upper illumination consisted of the rays from a 2 c.p. lamp passing through a circular opening 10 cm. in diameter and falling a distance of 120 cm.

The importance of L will be understood more thoroughly in connection with the conditions for size discrimination. If a chick is being trained to choose ⊙ 28+,[3] (a circle whose area

<hr />

[3] The dimensions of stimulus areas refer in square centimeters to the area.

is 28.2744 sq. em.), and to reject ⊙ 7+, unequal amounts of
light from the stimulus sources will be admitted to the electric
compartments. If the intensities of the two stimulus areas be
equalized, the compartment at the end of which the larger
circle appears will be the more highly illuminated. Without
the elimination of this factor of general illumination, the ex-
perimenter can not be certain that his animals are discriminat-
ing on the basis of size; they may be choosing the *lighter* com-
partment. To overcome this difficulty the upper illumination
was used and the elongation of the electric compartments,
O O O, figure 2, was introduced. The amount of upper illumi-
nation should therefore depend upon the degree of difference
between the two stimulus areas, and in a quantitative study,
where the difference is continually being reduced toward the
minimum of the animal's discriminative ability, the difficulty
practically disappears.

A further value of the upper illumination is economy of time
for the experimenter. It aids in emphasizing, from the first,
the visual factor which is being tested and thus prevents the
animal from acquiring a habit of discrimination which later
must be inhibited and replaced by a different habit. After an
animal once acquires a definite way of reacting to stimuli, no
little time and pains are required to make it change its mode
of response.

With the elongation of the electric compartments appears
another difficulty differing somewhat from the matter of general
illumination. This is the problem of the chick's optimal focal
distance. It is quite possible that, for a stationary stimulus,
the discrimination chamber of this apparatus is too far away.
The anatomy of the eye as well as the behavior of the animal
should be considered in connection with this problem. The
matter of distance perception, however, falls without the scope
of the present task.

II. PROBLEM, METHOD, AND TECHNIQUE

1. The chicks

The experiments reported in this paper were made with
about 25 chicks belonging to three different groups. The first
group, originally consisting of 10 chicks, was secured from a

poultry breeder when the chicks were about two days old. The second and third groups were artificially incubated in the laboratory. All of the chicks used were of the Barred Plymouth Rock variety. The matter of caring for the birds and keeping them healthy was one of the most serious difficulties which I had to overcome. On the whole, I found it more satisfactory to use the laboratory hatched chicks.

The most common ills were bowel trouble and "leg weakness." Both types of disease were chiefly due to improper feeding, temperature, and ventilation. My experience leads me to conclude that chicks in close confinement must be fed on "starving rations." A few individuals of group 3 survived until the weather became warm enough to get them out of doors during a few hours on favorable days. When this plan was first tried the birds were in poor condition. Two-thirds of the group had already died. But as soon as the survivors were placed out of doors their physical condition began to improve, and I was able to do nearly three times the amount of experimental work that I could formerly accomplish. Apparently the factors that healthy laboratory chicks require is an abundance of sunlight and fresh air with an opportunity to work for their living.

The "leg weakness" is a type of disease which had previously given trouble in the laboratory. The leg joints become enlarged, the toes curl out of shape, the birds cannot stand, and they move about only with great difficulty. This trouble ultimately carried off nearly all of the birds which did not succumb to bowel trouble. In the case of one brood I think it was the result of excessive heat in the brooder. In other cases it was probably due to overfeeding. More often, perhaps, it was due to a combination of both conditions. The birds which first showed signs of this weakness were the largest and apparently strongest of the flock. There was no evidence of it among the chicks of the third group, which were fed very sparingly, while the temperature of the brooder was carefully regulated.

2. The problem

The matter of health among the chicks turned out to be a problem which had not been anticipated. However, it did not prevent work toward the solution of the primary problem. The

task originally planned was a study of the chick's discrimina-
tive ability between sizes, forms, and brightnesses, but, owing
chiefly to these unfavorable conditions, little consideration has
been given to the third factor. The present paper is a prelim-
inary report of a detailed investigation which the writer hopes
to complete within a few years.

As far as the study goes, the aim has been to make it inten-
sive and quantitative. In the matter of size and form, the
question has been, not merely: Can the chick discriminate
between stimuli which differ from each other with respect to
one of these factors, but What is the least difference that it
can discriminate? Breed's work [4] has indicated that chicks *can*
discriminate on these bases. The work of Katz and Révész [5]
suggests the same possibility. My original plan, therefore, was
to test this matter quantitatively and to determine the chick's
threshold of difference for each of these factors.

With respect to size, I have carried out my original plan
without any essential changes, but in the case of form, I was
forced to abandon the plan with which I started. In a short
time it appeared that proper responses to stimuli differing from
each other only with respect to form were not so readily acquired
as reactions to size differences. After I had tried in vain for
several weeks to train different subjects to discriminate between
a circle and a triangle which were equal in area, the nature of
my problem was markedly changed. It was clearly necessary to
determine whether the chick, under the conditions of this ex-
periment, could perceive form.

Finally, another aspect of the problem which quite naturally
appears in an investigation of this sort is that of the relative
value of visual size, form and brightness. My earlier results
with forms, negative beyond all doubt, emphasized the desir-
ability of considering the factors in combination as well as in
isolation. In its normal life the chick is not compelled to rely
upon a single visual factor, but, on the contrary, it relies upon
a natural combination of visual qualities. It thus seemed
important to start with complex stimuli and from these grad-

---

[4] Breed, Frederick S. The development of certain instincts and habits in chicks.
Behavior Monographs, 1911, vol. 1, no. 1, S. N. 1; also Reactions of chicks to opti-
cal stimuli. *Jour. Animal Behavior*, 1912, vol. 2, pp. 280-295.
[5] Katz, D. and Révész, G. Experimentell-psychologische Untersuchungen mit
Hühnern. *Zeit. f. Psych. u. Physiol. d. Sinnesorgane*, 1909, Bd. 50, S. 93.

ually to eliminate the inequalities which were not wanted, until only the visual factor in question remained.

3. Method and technique

These changes in the problem are closely allied with the mode of procedure. The mechanical phase of my method appears in the description of the apparatus, but it does not fully explain the application of this procedure to the study of the chick's visual perception. This topic might well be considered in two parts:—the one dealing with the mechanism, the *objective aspect*, and the other relating to the plan of procedure, the *personal aspect* or *technique*. In this report I shall not attempt to make such a sharp distinction, for while the two topics are, in many respects, clearly distinct, I find them so closely interrelated that it is impracticable to consider them separately. In general, however, I shall devote the first part of this section primarily to method, and in the latter part, the discussion will be continued more from the standpoint of technique.

The plan of the apparatus in relation to the chick is to provide conditions both desirable and undesirable. Either nest box includes those factors which the chick wants. It provides food, light, warmth and companionship. The experiment box is arranged to make the chick want to get out. In the entrance box the chick is closely confined; in both the entrance and discrimination chambers the floors are wet; the entire experiment box, exclusive of the nest boxes, provides faint illumination, little warmth, no food and no companionship. When a chick, familiar with the nest boxes, is placed in the entrance box its natural desire is to get back to one of the nest boxes. Its problem, then, is to learn how to get to the desirable part of the apparatus.

The two visual stimuli which are displayed on the stimulus shifter indicate to the animal which nest box to choose. During the training series, both electric compartments are identical except for the difference between the two stimulus areas. Since the animal wants to reach the nest box it will try to find a way of accomplishing this end.

Each chick was taught the way of escape to the nest box by means of 20 preliminary trials. The entrance to the nest

box on that side where the *right* stimulus appeared was open; the sliding door closed the entrance from the electric box where the *wrong* stimulus was presented. The chick was allowed to go now to one, now to the other nest box, in irregular sequence until it had found its way 10 times to each. It was thus made familiar with nest boxes and the experiment box.

By displaying, always on the side of escape, the stimulus which the chick was later to be trained to choose, the animal was occasionally aided in acquiring a perfect habit.[6] This condition was especially noticeable in the experiments on size discrimination. In this case a circle 6 cm. in diameter always appeared in that electric compartment from which the subject escaped. At the end of the preliminary series a few chicks had acquired a perfect response to this condition of ⊙ 28+—⊙ 7+ discrimination.[7] This perfect ⊙ 28+—⊙ 7+ habit, however, may not mean that size was the basis of choice. It is quite possible that the birds chose the lighter compartment. Precaution was always taken to eliminate this possibility before size tests were completed, and control tests were carefully planned to make certain that it *had* been eliminated.

This preliminary work was followed by the training series. Both entrances to the nest boxes were now closed, and the only cues that remained to aid the chick to reach the nest box were the two optical stimuli. Continuing the example of size discrimination, ⊙ 28+ was the positive sign, ⊙ 7+ was the negative sign of escape from the experiment box. At this point in the training the electric shock was introduced. If a chick chose ⊙ 7+, *i.e.*, stepped upon the wires of that compartment, it was shocked. This was done by momentarily closing the key, Z, (figure 1). A single shock was usually given, but if the behavior of the bird indicated that the shock had not been sensed, it was repeated. The wet floors of A and B served to regulate the intensity of the shock. Great care was necessary to provide a shock that was an effective punishment yet not severe enough to frighten the animal. Care in the manipulation of the shock was also essential. The results of weeks of work could be destroyed in a moment through an error in the administration of punishment.

[6] A habit is termed perfect when a chick successively makes 20 correct choices.
[7] The stimulus demanding a positive response is named first; following this is the stimulus demanding a negative reaction.

It was quite common for chicks that were being trained to go beyond the door to the nest box and crowd up to the stimulus at the end of the compartment. If the animal were allowed to do this it spent considerable time and energy trying to get through the illuminated stimulus plate. A thin plate of glass was placed across each compartment at a point just beyond the exit. The chicks could thus see through the stop but could not go beyond it. They thus were stopped near the exit so that they might learn more readily how to escape. As soon as they had acquired a mode of escape and had ceased trying to reach the stimulus, the glass plates were removed.

After a perfect habit had been acquired the amount of difference between the two stimuli was decreased. When the ⊙ 28+—⊙ 7+ discrimination, for example, was perfect, the condition was changed to ⊙ 28+—⊙ 9+. The large circle was thus the standard which remained constant. The smaller circle was the variable, which, after each perfect reaction, was successively increased in size until the animal could no longer choose correctly. This limit of correct choices was thus accepted as the chick's threshold of difference.

Table 1, page 74, provides for a series of stimulus plates that will enable the experimenter to make the most satisfactory changes in the variable stimulus. The changes in diameter can well be as great as 5 mm. between ⊙ 7+—and ⊙ 12+ when used with a standard ⊙ 28+. Above ⊙ 12+ the diameter of the variable should be successively increased only by 1 mm. The set of plates with which I started included a group between ⊙ 19+ and ⊙ 28+ varying in diameter by 1 mm., but provided only a ⊙ 16 between ⊙ 12+ and ⊙ 19+. A similar scale was provided between ⊙ 50+ and ⊙ 63+ but there were no variables between ⊙ 28+ and ⊙ 50+. After a little preliminary work, however, I discovered that a different scale of variables was necessary, and in table 1 I present the sizes which my experience leads me to regard as essential. Unless he wishes to make a study of that particular problem, the experimenter, in using variables differing in diameter by only 1 mm., must be alert to see that the natural discrimination of his subjects is not improved by training.

During the experiments with the first group of chicks, I was seeking to get a method as much as to train the birds. I can

HAROLD C. BINGHAM

RECORD SHEET.

Subject — 9 — Date 12/7/'11 – 1/2/'12 Experiment Form Perception

Tests → / Series ↓	1	2	3	4	5	6	7	8	9	10	R	W	REMARKS Average Time
A	l	r	l	r	l	r	l	r	l	r			
B	r	l	r	l	r	l	r	l	r	l			
1	r E-29	l 0-6	r E-59	l 0-19	r E-125	l 0-120	r E-56	l E-95	r E-65	l 0-44	4	6	61.8°
2	l 0-4	l 0-24	0-36	0-30	E-1-62	0-39	0-19	E-2-180	0-15	0-33	8	2	44.2
3	r 0-67	0-8	E-135	0-28	0-25	E-2-141	E-1-180	E-1-21	0-5	E-1-61	5	5	67.1
4	0-29	E-1-42	E-1-35	0-55	0-40	0-64	E-2-100	0-30	0-32	E-1-65	6	4	49.2
5	E-2-84	0-1	0-9	0-12	0-10	0 6	0-18	0-26	E-1-43	E-2-38	7	3	25.4
6	0-11	0-14	E-2-71	0-21	0-83	E-2-41	0-28	E-2-110	0-49	E-2-118	6	4	54.6
7	0-48	0-31	E-2 70	0-7	E-1-8	E-1-23	0-25	0-6	0-9	E-1-56	6	4	28.3
8	E-2-46	0-62	0-89	0-67	E-2 71	0-58	E-1-65	E-1-56	0-24	E-1-29	4	6	56.0
9	0-4	0-5	0-6	E-1-20	E-1-7	0-21	E-2-42	E-1-23	0-15	E-1-16	5	5	15.9
10	0-4	0-4	0-5	0-31	0-106	0-19	0-61	0-5	0-10	0-5	10	0	29.5
11	0-10	E-2-124	E-2-125	0-35	E-2-75	0-67	0-34	0-26	0-38	E-1-88	6	4	60.2
12	0-6	0-37	0 22	0-10	0-14	0-12	0-8	0-8	E-1-36	E-1-14	8	2	16.7
13	0-8	0-7	0-40	0-45	E-1-110	0 3	0-1-29	E-1-20	0-21	E-2-44	7	3	32.7
14	0-12	E-1-123	E-1-31	0-10	E-1-10	0-74	0-12	E-1-27	0-8	E-1-31	5	5	33.8
15	0-38	0-11	0-22	0-8	E-1-38	E-2-54	E-2-64	0-16	E-1-39	0-5	6	4	29.5
16	0-18	0-1	0-21	0-30	0-5	E-1-46	E-1-42	0-33	0-11	0-28	8	2	24.2
17	0-42	0-37	0-40	0-11	E-1-10	E-1-50	0-62	0-30	0-28	E-1-19	7	3	42.8
18	E-1-60	E-1-94	0-25	E-1 35	0-20	E-1-24	E-1-25	0-15	E-1-18	0-12	4	6	32.8
19	0-92	0-40	F-1-46	E-1-76	0-26	E-1-53	E-2-45	0-10	E-2-27	E-1-33	4	6	44.7
20	E-1-13	0-39	0-8	E-2-17	0-18	0-25	0-9	E-1-60	0-42	E-1-103	6	4	33.3
21	E-1-22	0-12	0-13	E-1-15	0-17	E-1-26	0-11	E-2-10	0-19	E-1-40	5	5	18.5
22	6-1-69	0-19	E-1-40	E-1-20	0-7	0-21	E-1-22	E-2-30	E-1-46	E-1-25	3	7	29.9
23	0-12	0-25	0-10	0-8	0-4	E-2-41	E-1-9	0-2	E-1-10	E-1-12	6	4	13.3
24	0-5	E-1-44	E-1-6	0-3	0-5	0-4	0-4	0-4	0-2	E-1-45	7	3	12.7
25	0-14	0-12	E-1-6	0-26	0-25	0-23	0-18	0-15	0-55	0-25	9	1	27.8

not here attempt to show how the method was developed. Only its final form can be presented. A form of *record sheet* had previously been used in the laboratory for tabulating experimental results in the discrimination method. This blank was well suited to my needs. It provides spaces at the top for recording the name or number of the subject, the date, and the experiment. Across the sheet are 10 vertical columns in which may be entered the result of each test. Each group of 10 tests constitutes a series. The sheet provides for records of 25 series with a space for two (A and B) preliminary or preference series. The result of 250 tests, therefore, may be put on one record sheet. The vertical columns headed *R* and *W* are for the total number of *right* and *wrong* choices made by the subject during a series of 10 tests. Another vertical column leaves space for remarks.

This record sheet does very well for keeping a concise summary of the experiments, but it does not enable one to keep

<div align="center">

TEST SHEET

</div>

Title of investigation,   Form: $\odot$ 28+—$\triangle$ 28+
Experimented on, 9
Harvard Psychological Laboratory, December 25, 1912
Record Sheet, 1; Series, 15

Test	Behavior	Record
1 r	$/\overline{/} - /// + ///$ $_{u}$	O–38
2 l	$/// + ///$ $_{u}$	O–11
3 r	$/\overline{/} + ///$ $_{u}$	O–22
4 r	$// + //$ $_{u}$	O–8
5 r	$/// - // \triangle^1 + ///$ $_{u}$	E–1–38
6 l	$/// - /// \triangle^2 + //$ $_{u}$	E–2–54
7 l	$// - /// \triangle^2 + ///$ $_{u}$	E–2–64
8 l	$// + //$ $_{u}$	O–16
9 r	$// + / \triangle^1 + //$ $_{u}$	E–1–39
10 l	$/ + //$ $_{u}$	O–5

6–4–29.5

REMARKS:—Tendency to choose by position,—*i.e.*, to go where it last escaped. Usually goes directly to other compartment when it has been shocked for wrong choice.

the details of the behavior. To do this I had a form of *test sheet* printed. It is headed by spaces for the title of investigation, the name of the subject, and the date; also there are spaces for reference to the *record sheet* and the particular series of the *record sheet* which the *test sheet* contains. The 10 tests, (horizontally arranged on the record page), appear vertically on the test page. After each one is a space for recording the details of the animal's behavior. At the right of the page is a narrow column for recording the results of the test,—whether or not an error was made, and the time for choosing. At the bottom is a space for remarks, where the record is always totalled and averaged,—total number of right and wrong choices and average of time in seconds. The record and this part of the remarks are transferred to their proper spaces in the record sheet.

The manner of recording the chick's behavior is illustrated in the accompanying *test sheet* which is a record of an actual series of tests. I used a set of symbols which enabled me to follow fairly accurately the movements of an animal while in the discrimination chamber. Herewith is presented the key to the symbols used in these experiments:

1. $+$ = Approach to *right* compartment.
2. $-$ = Approach to *wrong* compartment.
3. $/$, $//$, $///$ = Degree of attention based on behavior and time. A horizontal bar above any one of these symbols indicates unusually long time in this locality. For example,
   a. $\begin{cases} +/ = \text{Brief consideration of } \textit{right} \text{ stimulus area.} \\ -/ = \text{Brief consideration of } \textit{wrong} \text{ stimulus area.} \end{cases}$
   b. $\begin{cases} +// = \text{Longer consideration of } \textit{right} \text{ stimulus area.} \\ -// = \text{Longer consideration of } \textit{wrong} \text{ stimulus area.} \end{cases}$
   c. $\begin{cases} +/// = \text{Close consideration of } \textit{right} \text{ stimulus area.} \\ -/// = \text{Close consideration of } \textit{wrong} \text{ stimulus area.} \end{cases}$
   d. $\begin{cases} +\overline{///} = \text{Long time before and close consideration of } \textit{right} \text{ stimulus area.} \\ -\overline{///} = \text{Long time before and close consideration of } \textit{wrong} \text{ stimulus area.} \end{cases}$
   e. $\begin{cases} +\overline{/} = \text{Long time before but slight consideration of } \textit{right} \text{ stimulus area.} \\ -\overline{/} = \text{Long time before but slight consideration of } \textit{wrong} \text{ stimulus area.} \end{cases}$
4. ⁄⁄⁄⁄⁄⁄⁄⁄⁄⁄⁄ = Attention at entrance end; indifferent to stimulus areas.
5. $\wedge$ = Approach on wires before *right* stimulus followed by retreat.
6. $\vee$ = Approach on wires before *right* stimulus followed by wrong turn.
7. $\triangle$ = Approach on wires before *wrong* stimulus followed by retreat.
   a. $\triangle^1$ = One shock.
   b. $\triangle^2$ = Multiple shock.
   c. $\triangle^0$ = No shock.
8. $\underset{\smile}{O}$ = Turn around, right to left; $\overset{\smile}{O}$, left to right.

9. ∽ = Partial turn around, right to left; ∾, left to right.
10. ⑃ = Position directly before division between each compartment; by turning head either stimulus area is visible.
11. ⑅ = Escape to nest box.
12. E = Error in choosing; this is followed by time in seconds.
13. O = Correct choice; this is followed by time in seconds.

The preliminary series were begun during the second week, usually when the chicks were 10 days old. The experiments were always conducted during the forenoon between the hours of eight and twelve. I believe the best results would be obtained from chicks if the work were begun earlier than eight. Chickens naturally start out early in the morning for their food. That is the time when they are most active. My observations do not wholly agree with Breed's conclusion that "hunger did not play a more important part than the reaction to confinement and solitude." [8] My best results came when I took the chick early in the morning and allowed it to earn its breakfast. The chick from which I received the best results reached the stage where it apparently took pleasure in the experiments. When I placed it in the apparatus it regularly began to give the characteristic "food twitter." This twittering was continued all of the time the bird was choosing and after it had escaped to the nest box where I was careful always to have a little food.

In the matter of rewarding with food, however, great care is necessary. A three-weeks-old chick will "fill up" in a very short time and then experimental work is difficult. I was careful to have only a few grains scattered in the litter of the nest boxes so that the chick had to work to find them. After getting this plan somewhat perfected I found that a chick could be given as high as 50 trials with no more difficulty than was previously common in 20 trials.

Until the chicks were five or six weeks old it was found best to give them no more than one series daily. After they reached this age the number of tests could be increased without harmful results. The subjects had usually learned to solve their problems by this time so that they expended much less energy than they did during the earlier tests. Moreover, the experimenter had an opportunity to select from his group the most promising subjects to which he could devote more time.

---

[8] *Behavior Monographs*, vol. 1, no. 1, S. N. 1, p. 47.

4. *Importance of method*

In the preceding section I have discussed in considerable detail the method and technique of my experiments. I do this because I believe an accurate solution of an animal problem depends upon the adoption of a favorable method. It is one of the greatest tasks that confronts the experimenter. He must use an apparatus by means of which he can accurately control the conditions of his study. He must also show alertness by controlling these conditions in such a way that his animals behave normally. Much animal stupidity, so-called, is really a reflection of human ignorance. Experimenters frequently lack animal intelligence by setting human problems for an animal to solve.

An animal frequently shows ingenuity in an unexpected direction, and if the experimenter be not alert he misses the most important part of the behavior. How many times this is the case, we cannot tell, for we only know of the cases where we did not miss the significant fact. A perfect method would make it impossible for the animal to pick up cues that were not intentionally offered by the experimenter. But it is through experience that we approach a perfect method for there is always the possibility of finding defects even in the best methods.

The importance of method was impressed upon me very forcibly through an incident in my experiments with the first group of chicks. I had inexcusably blundered by making the original conditions of discrimination too difficult for the birds. They were being tested on ⊙ 28+—⊙ 7+ discrimination. The subjects were allowed to go through the discrimination chamber and experiment box during the preliminary tests without regard to the position of the right or wrong stimulus; that is, both exits were open. When the training series were begun the brightness of the two stimuli were made markedly unequal and were irregularly varied *from the first*.

The experiment was begun with six subjects. As a partial result of my initial bungling, I had, at the end of a few days, only subjects 2 and 3 in suitable condition for experimental work. At the end of two and one-half weeks No. 2 gave up, but No. 3 persisted. At the end of the 24th series it had successively made three perfect series (see table 2). At the end of four more series it had reacted perfectly to the ⊙ 28+—⊙ 9+

discrimination. The variable was continually increased by 5 mm. (diameter) until the condition ⊙ 28+—⊙ 19+ was reached

TABLE 2

Subject: 3. Hatched: 10/3?/'11. Sex: Undetermined

Series*		Date	Right	Wrong	Time†
		⊙ 28+—⊙ 7+ *Discrimination*			
1–21	(1–21)	Oct. 12–27	. .	. .	. .
22	(22)	" 28	10	0	55
23	(23)	" 30	10	0	41
24	(24)	" 30	10	0	29
		⊙ 28+—⊙ 9+ *Discrimination*			
1	(1)	Oct. 30	10	0	62
2	(2)	" 31	9	1	79
3	(3)	" 31	10	0	103
4	(4)	Nov. 1	10	0	55
		⊙ 28+—⊙ 12+ *Discrimination*			
1	(6)	Nov. 2	7	3	71
2	(7)	" 3	9	1	93
3	(8)	" 3	10	0	50
4	(9)	" 4	10	0	52
		⊙ 28+—⊙ 15+ *Discrimination*			
1	.(11)	Nov. 4	6	4	112
2	(12)	" 6	9	1	68
3	(13)	" 6	8	2	44
4	(14)	" 6	8	2	51
5	(15)	" 7	9	1	52
6	(16)	" 7	9	1	40
7	(17)	" 7	8	2	41
8	(18)	" 8	10	0	52
9	(19)	" 8	10	0	62
		⊙ 28+—⊙ 19+ *Discrimination*			
1	(21)	Nov. 8	8	2	49
2	(22)	" 9	8	2	49
3	(23)	" 9	8	2	90
4	(24)	" 9	10	0	50
5	(25)	" 10	8	2	78
6	(26)	" 10	10	0	53
7	(27)	" 11	10	0	47
		⊙ 28+—⊙ 23+ *Discrimination*			
1	(6)	Nov. 11	8	2	58
2	(7)	" 13	8	2	116
3	(8)	" 14	10	0	41
4	(9)	" 15	8	2	45
5	(10)	" 15	10	0	16

* Numbers in parentheses refer to series on record sheet.
† Average time for series given in seconds.

TABLE 2—*Continued*

SUBJECT: 3.　HATCHED: 10/3?/'11.　SEX: UNDETERMINED

Series*		Date	Right	Wrong	Time†
		⊙ 28+—⊙ 24+ *Discrimination*			
1	(21)	Nov. 17	10	0	22
2	(22)	" 17	9	1	30
3	(23)	" 18	10	0	16
4	(24)	" 18	10	0	11
		⊙ 28+—⊙ 25+ *Discrimination*			
1	(11)	Nov. 21	9	1	22
2	(12)	" 21	10	0	16
3	(13)	" 21	9	1	17
		⊙ 28+—⊙ 26+ *Discrimination*			
1	(16)	Nov. 22	10	0	15
2	(17)	" 22	9	1	24
3	(18)	" 23	7	3	45
4	(19)	" 23	10	0	23
		⊙ 28+—⊙ 27+ *Discrimination*			
1	(21)	Nov. 23	8	2	20
2	(22)	" 23	8	2	25
3	(23)	" 24	6	4	33
4	(24)	" 24	10	0	11
5	(25)	" 24	9	1	30
		⊙ 28+—⊙ 28+ *Discrimination*			
1	(1)	Nov. 25	10	0	?
2	(2)	" 25	6 (eraek closed)	4	?
3	(3)	" 25	0	5	?
		⊙ 28+—⊙ 23+ *Discrimination*			
1	(16)	Nov. 27	5	5	62
2	(17)	" 27	5	5	59
		⊙ 28+—⊙ 19+ *Discrimination*			
1	(18)	Nov. 28	3	7	71
		⊙ 28+—⊙ 15+ *Discrimination*			
1	(19)	Nov. 28	9	1	60
		⊙ 28+—⊙ 19+ *Discrimination*			
1	(20)	Nov. 29	6	4	73
2	(21)	" 29	5	5	83
3	(22)	" 30	7	3	31
4	(23)	" 30	7	3	22
5	(24)	" 30	5	5	23
6	(25)	Dec. 1	5	5	27

* Numbers in parentheses refer to series on record sheet.
† Average time for series given in seconds.

after which the diameter of the variable was changed by incre-
ments of 1 mm. The perfect responses continued almost as
regularly as the variable was increased. Finally the behavior
of the chick indicated that it was discriminating between
⊙ 28+ and ⊙ 27+ (see record of November 23 and 24).

A ⊙ 28+—⊙ 27+ discrimination was incredible, for the human
eye could scarcely detect a difference between a 28+ sq. cm.
circle and a 23+ sq. cm. circle. The only thing to do was to
test the chick on ⊙ 28+—⊙ 28+ discrimination. The result was
a perfect series. (See record 1, November 25.) Then I began
to look for the cue on which the chick relied. At last I noticed
a small crack where the outside extension of the electric box
was joined to the experiment box. A similar crack appeared
on both sides in corresponding positions, hence it seemed that
in this factor there could be no clue by means of which the
chick was guided in its choice of the *right* compartment.

Close inspection, however, proved that in these two minute
cracks lay the cue by means of which the chick had been dis-
criminating. Where the rabbeted edges of the shifter and
tracks rubbed, there was a bright edge, and wherever the shifter
rested, this bright surface was covered. Thus when the shifter
was at the left, the right end of the track was uncovered, and
from this uncovered part was reflected some of the light rays
from the upper illumination. A small portion of this reflected
light could enter the crack on the left side. Now, when the
standard circle was presented at the left, it happened that the
shifter was moved to the right; when the standard appeared at
the right, the shifter stood at the left. As a result, the crack
that was illuminated was always the one where the standard
circle was displayed; the other crack, being reached by no
reflected light, was always dark.

Noticing this *slight* variation in the condition of illumination
in the two compartments, and desiring to ascertain by what
clue the chick was choosing, I closed the small cracks through
which the light was reflected. The effect of this change appears
in the records following the first on November 25. The perfect
reactions abruptly stopped with the closing of the cracks; out
of 15 tests there were only six correct responses. As appears
in the subsequent part of table 2, I continued the experiment,
with the cracks stopped, by reducing the area of the variable to

23+, (November 27), then to 19+ and finally to 15+ before the chick again began to react correctly to the stimuli. When the ⊙ 28+—⊙ 19+ discrimination was again presented, the subject was able to choose correctly in little more than half of the tests. The physical condition of No. 3 on December 1 made it necessary to abandon further work. Up to that date it had appeared in all respects normal, but the final series was conducted with great difficulty on account of the common "leg-weakness" which had suddenly developed. With the appearance of this disease, the experiment was abruptly closed.

The chick, then, had detected a faint streak of light, not more than 6 mm. long and less than 1 mm. wide,—an illumination so small that not only I but others who were working in the laboratory had quite overlooked it. By considering the amount of light that came from the upper illumination, the poor reflecting surface of a steel strap worn only moderately bright, and the narrow surface from which the light was reflected, (not more than 1 cm. in width), the reader can judge how insignificant this strip of light would appear. It was clearly a case of the chick "outguessing" the experimenter.

III. SIZE PERCEPTION

1. Discrimination between unequal circles

The foregoing discussion of method suggests the nature of the difficulties which were encountered in the early experimental work. No trustworthy results were secured until after the crack of light was discovered. By this time No. 3 was the only subject of the first group that was still working. The later experiments with this chick indicated that the early discrimination had been made on the basis of size difference, but as the variable became larger and the discrimination correspondingly harder, No. 3 began to look for other cues and happened upon the one which has been described.

A glance at table 2 suggests the point where No. 3 ceased to discriminate between the two size stimuli. After the control tests, ⊙ 28+—⊙ 28+ discrimination, during which the crack was stopped, the chick's response to ⊙ 28+—⊙ 23+ was tested. The results were decidedly negative since the *right* stimulus was chosen no more than chance would allow. The response to

⊙ 28+—⊙ 19+, having only three right choices, was even more negative, but when the ⊙ 28+—⊙ 15+ discrimination was tested, the results were clearly positive. The standard was chosen nine times and the variable was chosen only once. Here is probably the place where, in the earlier training, the new cue first figured. While the average results of the tests with the ⊙ 19+ variable are slightly in favor of the larger stimulus, I believe the fact should not be emphasized, for the larger circle was chosen in 60 trials only five more times than would have occurred had chance alone determined the choices.

Table 3 summarizes the results of my investigation on the chick's perception of size. In some cases the results are not so clear cut as one might wish, but this fact is due to the uncertainty of health among the birds which made it advisable to hurry the tests, without waiting in some cases for the acquisition of perfect habits, in order to take the chicks to their limit in discrimination.

By considering not only the right-wrong records but also the peculiarities in behavior which cannot be presented in tabular form, I am convinced that the largest variable the chick can distinguish, under the conditions here described, from a standard ⊙ 28+ lies somewhat above ⊙ 15+. The quantitative measurements on the basis of right choices points strongly to this conclusion. Every subject, excepting 7 and 20, succeeded in making at least 88% of correct choices in a series when the ⊙ 28+—⊙ 15+ discrimination was required. Even in the case of the two exceptions, 7 and 20, an efficiency of 70% was acquired. But more convincing still is the fact that two chicks, 3 and 17, reached 90%, and two, 16 and 21, made perfect series.

The time used in choosing is a factor which offers a means of measuring quantitatively the chick's threshold of discrimination. It should not be unduly emphasized for it is not wholly reliable, yet in these experiments it tends to substantiate the conclusion which has been based upon the percentage of right choices. Since the animal is less acquainted with the conditions during the ⊙ 28+—⊙ 7+ discrimination as compared with the ⊙ 28+—⊙ 15+ discrimination, it would be expected, other things remaining constant, to choose more readily during the later tests. Furthermore, the increase in age and activity should enable it to choose more rapidly during the later tests.

TABLE 3

Discrimination Between Unequal Circles

Series	No. 3[1] 28+ R	28+ W	7+28+ R	7+28+ W	28+12+ R	28+12+ W	28+15+ R	28+15+ W	No. 6♂ 28+ R	28+ W	7+28+ R	7+28+ W	28+12+ R	28+12+ W	28+15+ R	28+15+ W	No. 7♂ 28+ R	28+ W	7+28+ R	7+28+ W	28+12+ R	28+12+ W	28+15+ R	28+15+ W	No. 15♂²[2] 28+ R	28+ W	7+28+ R	7+28+ W	28+12+ R	28+12+ W	28+15+ R	28+15+ W	No. 16♂²[2] 28+ R	28+ W	7+28+ R	7+28+ W	28+12+ R	28+12+ W	28+15+ R	28+15+ W
1					5	5	9	1	7	3			8	2	8	2	8	2			10	0	7	3	9	1			10	0	7	3	9	1	8	2			10	0
2					8	2		3	9	1			8	2		4	6	4			9	1	7	3							7	3								
3					6	4			9	1			8	2			7	3			7	3		4							8	2								
4					8	2			8	2			6	4			9	1			8	2																		
5					9	1			10	0			8	2			9	1			9	1																		
6					6	4			9	1			6	4			9	1			8	2																		
7					10	0			8	2			8	2			10	0																						
8									6	4							8	2																						
9									9	1							10	0																						
10									10	0							10	0																					–	
11									8	2							10	0																						
12									10	0							10	0																						
13									10	0							10	0																						

[1] Preceded by tests which were ruled out on account of the crack of light.
[2] The record for ☉28+ —☉7+ was preceded by 13 series in which the light factors were combined; the record given represents the first series after all factors except size were eliminated.
[3] Followed by ☉28+ —☉19+ in which No. 3 failed.
[4] Tests were hurried on account of physical condition of subject.

TABLE 3—*Continued*

DISCRIMINATION BETWEEN UNEQUAL CIRCLES

Series	No. 17♀² 28+ 7+ R	W	No. 17♀² 28+ 12+ R	W	No. 17♀² 28+ 15+ R	W	No. 18♂² 28+ 7+ R	W	No. 18♂² 28+ 12+ R	W	No. 18♂² 28+ 15+ R	W	No. 20♂(?)² 28+ 7+ R	W	No. 20♂(?)² 28+ 12+ R	W	No. 20♂(?)² 28+ 15+ R	W	No. 21♀² 28+ 7+ R	W	No. 21♀² 28+ 12+ R	W	No. 21♀² 28+ 15+ R	W
1	10	0	10	0	8	2	8	2	10	0	8	2	9	1	8	2	7	3	7	3	10	0	10	0
2					9	1					5	5					7	3					7	3
3											8	2					6⁶						8	2
4											5⁵												8	2
5																							6	4
6																							10	0
7																								
8																								
9																								
10																								
11																								
12																								
13																								

² The record for ⊙ 28+ —⊙ 7+ was preceded by 13 series in which the light factors were combined; the record given represents the first series after all factors except size were eliminated.

⁵ Became discouraged.

⁶ Tests ended on account of physical condition of subject.

Table 4, however, shows that this was not the case. The total average in seconds of time for ⊙ 28+—⊙ 7+ was 11. This time was increased for ⊙ 28+—⊙ 12+ to 16, and for ⊙ 28+—⊙ 15+ to 20 seconds.

TABLE 4

AVERAGE TIME FOR CHOOSING

Subject	⊙ 28+—⊙ 7+	⊙ 28+—⊙ 12+	⊙ 28+—⊙ 15+
6	15″	13″	7″
7	22	59	55
15	8	5	31
16	30	28	11
17	3	8	13
18	4	3	20
20	3	13	11
21	6	2	9
Average	11	16	20

It might be urged that this time average changed during the course of the experiments on account of the physical condition of the chicks. I do not believe this was the cause. Consider the record made by No. 21. This chick was one of the few which was turned out of doors, where its physical condition improved. That it was not weak at the conclusion of the work on size discrimination is suggested by the fact that it was put through nearly 1500 subsequent tests on form vision. This chick, as shown in table 3, made perfect records in ⊙ 28+—⊙ 15+ discrimination. Its time, according to table 4, averaged six seconds during the ⊙ 28+—⊙ 7+ tests, only two seconds in the ⊙ 28+—⊙ 12+ test, and nine seconds in the ⊙ 28+—⊙ 15+ tests. Evidently the chick was slower in the ⊙ 28+—⊙ 7+ tests where it was learning, its time was *not* increased when the variable was increased to ⊙ 12+ because the discrimination was still easy, but the time *was* increased when the more difficult discrimination, ⊙ 28+—⊙ 15+, was required.

The detailed behavior of the birds, furthermore, tends more firmly to establish the explanation offered. To illustrate how the behavior differed under the conditions of *easy* and *difficult* discrimination, two test sheets are presented.

TEST SHEET 1

Title of investigation, Size: ⊙ 28+—⊙ 7+
Experimented on, 21
Harvard Psychological Laboratory, February 28, 1912
Record Sheet, 1. Series, 6

Test	BEHAVIOR	Record
1 l	// + /// ‖	O–4
2 l	+ /// ‖	O–5
3 r	+ /// ‖	O–2
4 l	+ /// ‖	O–1
5 r	+ /// ‖ ·	O–2
6 r	+ /// ‖	O–2
7 l	+ /// ‖	O–2
8 r	+ /// ‖	O–2
9 l	+ /// ‖	O–2
10 r	+ // ‴‴ ‖ ·	O–10

10–0–3.2

Test sheet 1 shows that No. 21 lost no time on entering the discrimination chamber, but went *directly* in every case to the correct stimulus where it entered the electric compartment and escaped to the nest box. Its final record in this series was 10 correct and no wrong choices, with an average time of 3.2 seconds. Test sheet 2 shows a different condition. No. 16 was discriminating between ⊙ 28+ and ⊙ 12+. In the first test the chick was quiet for a long while on entering the discrimination box; then it went to the *wrong* side where it stopped momentarily about two-thirds of the distance between the back of the discrimination box and the beginning of the electric wires. It then turned to the left, went close to the left electric compartment, hesitated, and entered only to turn to the right and come out. After looking closely again at the *wrong* (right hand) stimulus it turned back to the *right* (left hand) compartment and escaped. The behavior was somewhat similar in the second test except that in turning away from the *wrong* stimulus which

TEST SHEET 2

Title of investigation, Size: ⊙ 28+—⊙ 7+
Experimented on, 16
Harvard Psychological Laboratory, March 6, 1912
Record Sheet 1; Series 16

Test	Behavior	Record
1 l	$\overline{///} - // + /// \vee - \overline{///} + ///$ "	O–47
2 r	$/// - // \underset{\sim}{\bigcirc} + ///$ "	O–38
3 l	$\overline{///} + - + // - \overline{/\,\triangle^1} + - // \triangle^1 + //$ "	E–2–58
4 l	$// + \overline{///} \wedge \underset{\sim}{\bigcirc} - /// + ///$ "	O–35
5 l	$/// + ///$ "	O–11
6 r	$/// - \overline{//} // \triangle^1 + ///$ "	E–1–21
7 r	$// + /// - /// \underset{\sim}{\bigcirc} + ///$ "	O–22
8 r	$+ ///$ "	O–5
9 l	$+ /// \overset{-}{\underset{\sim}{\bigcirc}} - /// \overset{=}{\bigcirc} + ///$ "	O–35
10 r	$// + ///$ "	O–10

8–2–28.2

this time was at the left, the chick turned itself completely around, counter clockwise, and came up to the *right* stimulus. The third test shows that No. 16 made two errors for each of which it was shocked. Test 9 indicates where the chick made two complete turns,—one counter clockwise from the *right* compartment which this time is at the left side, and one clockwise turn from the *wrong* or right hand compartment.

These two test sheets have been selected with an idea of showing as marked contrast as possible, that the reader may see how important is the chick's behavior during each test and series. The first shows that No. 21 had no difficulty in choosing the proper stimulus. The second indicates that No. 16 was comparing both stimuli and using considerable care in choosing, although it made two errors. The choice record would indicate poor discrimination, but the behavior shows that the bird was really discriminating. The time contrast also stands out in the

two series. These two series cannot be called typical of my experiments, yet, on the whole, they fairly represent the principles of the chick's mode of discrimination.

On the basis of choices, behavior, and time, it thus appears that the chick's limit in discrimination from a standard ⊙ 28+ lies somewhere between ⊙ 15+ and ⊙ 19+. To express the relation in terms of centimeters instead of square centimeters, the size in diameter of the variable is above 4.5 but below 5, that of the standard is 6. *The threshold of difference with a standard 6, therefore, is one-fourth to one-sixth.*

2. Technique in experiments on size

After working only a short time on size perception I was convinced that the chick which was being trained should be aided by having the differences between the two visual stimuli emphasized by a combination of light factors which would aid in the earlier discrimination. Two stimulus areas, differing from each other with respect to one quality only, present to the animal a problem which is quite unnatural. Under natural conditions it relies upon combinations of many visual factors. The perception of an isolated visual quality is a human problem, not an animal problem.

After a little preliminary sparring, therefore, the chick which was being trained was first presented with two stimuli differing from each other with respect to size, form, and brightness. The stimulus to be chosen was a triangle larger and brighter than a circle. On account of these conditions the *right* stimulus appeared in the lighter compartment. The chick was thus trained to choose (1) the lighter compartment in which the stimulus area was (2) larger, (3) triangular, and (4) brighter. The process now was to remove, if possible, so gradually that the chick was aware of no changes, all of the inequalities between the two stimuli except size difference. This was not difficult to do. As is indicated in table 3, undesired factors were removed before the 14th series, and the single record that is given in the table for ⊙ 28+—⊙ 7+ discrimination is the first one in which the conditions were so arranged that the chick could not possibly choose on the basis of any factor other than size. As the table also suggests this was the first and only ⊙ 28+—⊙ 7+ series of this sort; the next deals with ⊙ 28+—⊙ 12+ discrimination.

That the discrimination was not by some factor or factors other than size, an explanation of my method during the control tests will show. In the main, the same procedure, but a more crude form, was carried out with Nos. 3, 6, 7, for with them the control method was conducted less definitely from the beginning of the training.

TABLE 5

CONTROL SERIES FOR ⊙ 28+—⊙ 7+ DISCRIMINATION

Nos. 15, 16, 17, 18, 20, and 21

March 4, 1912

Record Sheet 1. Series 14

Test	Source distance from		General illumination of	
	+ Stimulus	— Stimulus	+ Compartment	— Compartment
1 l	cm. 240	cm. 125	Uncontrolled except for upper illumination.	
2 l	240	125	"	"
3 r	240	125	Much darker: Covered with 2 thicknesses of ground glass.	Much lighter: Covered with thin sheet of plain glass.
4 l	240	125	Darker: Covered with 1 thickness of ground glass.	Lighter: Covered with 1 thickness of plain glass.
6 r	240	240	"	"
7 l	180	180	"	"
8 r	180	180	"	"
9 l	180	180	"	"
10 r	180	180	"	"

The plan of the control is concisely stated in table 5. The location of the source lamps was varied according to the plan of the second and third columns. The illumination of the electric boxes was controlled according to the last two columns. In tests 1 and 2, the + or *right* stimulus area was considerably brighter and that compartment was markedly lighter than the other. In tests 3 and 4 the *right* stimulus was brighter but the general illumination was reversed. The *right* compartment was kept slightly darker after the fourth test than the *wrong* com-

partment. In this respect the conditions were exactly reversed from those of all former series, but the chicks had, in earlier series, become accustomed to reversal of brightness. It was under these conditions that the records of chicks 15, 18, 20, and 21, as presented in table 3, were made. It is incredible that the discriminations occurred on any basis other than size difference.

IV. FORM PERCEPTION

1. *Literature*

On account of the contrast between the outcome of my study of the chick's discrimination of form differences and the results reported by earlier experimenters in the same field, it is desirable to preface the account of my experiment with a brief review of these preceding studies on form perception. I shall limit this review to a consideration of two papers; one by Katz and Révész [9] and the other by Breed.[10] In both papers positive results have been reported.

In its simpler form, the "Klebmethode" of Katz and Révész consists in pasting on a cardboard, kernels of grain at which the chicken's pecking response is to become inhibited. Among these "glued" kernels is scattered a different kind of grain which the bird is allowed to pick up. To illustrate, it was found by the experimenters that the birds preferred rice to wheat. Twenty kernels of rice were glued to the background and 10 grains of wheat were scattered among them. A series was recorded every time the chicken picked up the wheat. The bird was classed as "Fehlerfrei" when it had picked up the wheat without pecking at the rice. The observers had two quantitative measurements for the rapidity of learning: (1) The number of series necessary for a perfect reaction; (2) the number of reactions to rice. To make sure that the "errorless" birds did not avoid the rice by means of the glue which might be visible on the pasted kernels, the rice was scattered loosely upon the cardboard in the same manner as the wheat. The wheat was again eaten by the "errorless" birds and the rice was left. The discrimination, the authors concluded, was between wheat and rice.

---

[9] Katz, D. and Révész, G. Experimentell-psychologische Untersuchungen mit Hühnern, *Zeit. f. Psych. u. Physiol. d. Sinnesorgane*, 1909, Bd. 50, P. 93.
[10] Breed, Frederick S. Reactions of chicks to optical stimuli, *Jour. Animal Behavior*, 1912, vol. 2, pp. 280-295.

Having found that the chicken could learn to pick up wheat
and avoid rice, Katz and Révész sought to answer the question:
By what means does the bird discriminate between the two
kinds of grain?   Accordingly they began to test the chicken's
discrimination of sizes and forms.   Because the chickens could
be trained to eat only half-grains of rice when scattered among
whole grains, the authors were convinced that there was a dis-
crimination of size and form.   A little further study leads them
to conclude: "The chicken also discriminates between squares
and triangles.   Knowledge of this fact we secured through a
variation of the experimental procedure.   Out of green peas,
(some of which had been readily eaten), we cut three and four
cornered pieces.   On account of their moisture they could not
be glued down, so we laid the four sided-pieces upon a glass
plate and the three-sided pieces under it.   The chicken found
that the three-sided pieces could not be reached and soon ceased
to peck at them.   Then if we laid both forms upon the glass
plate, only the squares were picked up.   By means of the same
method we found that the chicken discriminates between trian-
gles and circles as well as squares and triangles."

The study made by Katz and Révész is open to the same
general objection with which this paper was opened.   They
have, in too many cases left the reader uncertain of the exact
conditions.   They have tried to do too much and have not
accomplished any one task; their report indicates carelessness
and indifference to details.   Such work makes an interesting
paper.   It is probably received more favorably by the majority
of readers than an intensive study of a problem.   After all,
however, this sort of superficial work does not get us anywhere.
No doubt the statement that "the chicken also discriminates
between squares and triangles" and "between triangles and
circles as well as squares and circles," holds true for the condi-
tions under which the experiment was made.   But from the
written account *one cannot tell what the conditions were.*   One
does not know, for example, the relative sizes of the different
forms.   Were they equal in area?   Was the square an inscrip-
tion of the circle or *vice versa?*   Was the diameter of the circle
equal to the height of the square or the altitude of the triangle?
These are some of the factors which *must be known* before one
can safely say that the chicken perceives form.   One could

truthfully state that an animal was discriminating between a circle and a triangle if it regularly chose the former even though the triangle were *seven* times as large as the circle, but it is quite improbable that the basis of discrimination in such a case would be anything other than size. Since such points were omitted from the written account, one suspects that the technique of the experimenters was decidedly imperfect. Even had they taken the precaution of equalizing the sizes, they would then have faced a problem still more difficult. Their task would then have been to show that the discrimination was not due to unequal stimulation of different parts of the retina. Furthermore, no information is offered as to the method of cutting these forms. It is a very difficult matter to cut green peas after any regular manner. How can the observers be certain that their subjects discriminated on the basis of form rather than irregularities in the surfaces? They make no mention of "check tests" to eliminate this possibility. It is because they leave vital points like these unmentioned and apparently unnoticed that one is led to class the experiment as a very superficial piece of work.

In the report by Breed on the reactions of chicks to form stimuli [11] the conditions of the experiment have been accurately presented. His chicks were given an opportunity to select a circle when appearing along with a square. Both stimuli were presented in a dark room by means of the illumination of screens consisting of two plates of flashed opal glass, over which were set mats of tin or cardboard containing the desired openings. Three chicks were used in this study, one of which, No. 76, "learned to discriminate two optical stimuli on the basis of difference of form."

Because his studies of the reaction of other chicks to similar stimuli yielded negative results, Breed attributes the positive reactions of No. 76 to a fortunate choice of subject. Unfortunately, however, he seems to have made no control tests to determine whether or not the distribution of light on the chick's retina was influential. An inversion of a square would cause no change in the distribution of light; such a change might have been produced by turning the square through 45°. A control test of this sort, however, is more easily made when a

[11] *Op. cit.,* pp. 290-293.

triangle is presented along with a circle.   Inversion of a triangle produces a marked difference in the distributions of the light which reaches the retina, yet the form of the stimulus is unchanged.

In the following report of my own tests on form discrimination, it will be noticed that I obtained results as positive as those of Breed when the apex of the triangle was at the top. When the position of the triangle was inverted, however, the perfect reactions ceased.   It was so difficult to get a chick to react positively when a square was used with a circle that I found it practicable to make the control test on the distribution of light only in the case of the circle-triangle reaction.   It is regrettable that Breed failed to make this control test in his experiments.

2. Experiments

The development of my system in the study of the chick's form perception followed, in general, that which occurred in my study of reactions to sizes.   Work on this visual factor, i.e., the discriminative ability between circles and triangles which are equal in area, was done with two of the second group of chicks, Nos. 9 and 11.   The latter became afflicted with "weak legs" after the 24th series, up to which time it had given no positive results.   The results from No. 9 might be regarded as slightly positive.

On the whole the results in table 6 show a preference for the circle.   Series 10 was perfect.   One contains 90% of *right* choices and several reached 70% or 80%.   It is not surprising that the chick became discouraged, since I had not yet adopted the plan of beginning with complex stimuli and working toward the simple.   A system of control similar to that described under size perception (p. 98) was used throughout the work.   The surprising feature is the high percentage of right choices on January 4 and 5 when the chick was becoming discouraged and frightened.   This condition resulted in a rush for one stimulus or the other as though "to get the choice over."   It appears that there was some sort of a difference between the two illuminations which tended to catch the eye of the rushing chick, but this was not clearly enough perceived for a dependable basis of discrimination.   Finally, this experiment did not definitely prove, even though we admit a preference for the circle,

TABLE 6
FORM PERCEPTION: ⊙ 28+—△ 28+
No. 9. Hatched: December 1, 1911. Sex: ♀

Series	Date	Right	Wrong	Time
1	Dec. 9	4	6	....
2	11	8	2	44.2
3	12	5	5	47.1
4	13	6	4	49.2
5	14	7	3	24.8
6	15	6	4 ·	54.6
7	16	6	4	28.3
8	18	4	6	56.8
9	19	5	5	15.9
10	19	10	0	29.5
11	20	6	4	60.2
12	21	8	2	16.7 ·
13	22	7	3	42.7
14	23	5	5	32.8
15	25	6	4	29.5
16	26	8	2 ·	24.2
17	27	7	3	42.8
18	27	4	6	32.8
19	28	4	6	44.7
20	28	6	4	33.2
21	28	5	5	22.
22	29	3	7	29.3
23	29	6	4	13.3
24	30	7	3	12.7
25	Jan. 2	9	1	27.8
1	2	7	3	30.9
2	3	5	5	25.4
3	4	7	3	12.5
4	5	8	2	4.6 (Rushing)
5	6	(Discouraged; rushed blindly to either stimulus.)		

that the chick perceived form. The preference may well have been due to the distribution of light or the unequal stimulation of different parts of the retina.

As has been earlier stated, the original plan was to test the minimum form difference a chick could perceive. The result of my investigation with No. 9 convinced me that it was necessary first to determine whether or not the chick perceives form. When the study of form perception was begun with group 3, the plan that was explained in the preceding chapter on size was adopted. That is, form, in the beginning, was made only one of other visual factors which were gradually eliminated as the experiment progressed. Only one chick, No. 21, gave anything like positive results. This bird, including 22 series on

size and brightness vision, was given more than 1500 tests.
The work done with it is the only experiment of value that
was made on form perception.

The experiment on form discrimination with No. 21 may be
divided into three parts: (1) A preliminary investigation;
(2) reactions to the triangle-circle and (3) reaction to the circle-
triangle. When the work on form perception was begun, I
had learned how to get much more work out of my subject
and, at the same time, less energy was called forth than in the
earlier tests. No. 21 knew me quite well by this time. It was
perfectly contented to leave the other birds in the chick-room
and go alone with me to the dark-room for work. The chief
reason for this was the fact that it always had its morning meal
in the dark-room. As soon as we reached the experiment room
it was fed a little chick food and allowed to run freely about
until the apparatus was made ready for the tests. While I
was preparing the apparatus, the chick would follow me about
the room (then lighted) twittering and contented, but if I left
it alone for a few minutes its dissatisfaction was made known
by loud and persistent peeping.

When everything was ready the chick was placed in the
apparatus. At this point the note in its voice changed very
noticeably. I cannot describe this sound, except that it was
a slightly modified, I believe it might be called a *modulated*,
"hovering twitter." Very commonly this peculiar sort of sing-
ing changed as the bird entered the discrimination chamber,
to the "food twitter" which was continued all the time it was
inspecting and comparing the two stimulus areas and, of course,
after it had entered the nest box for there it was rewarded by
finding a few grains scattered in the litter. In this manner a
series could be completed in about 15 minutes after which the
chick was taken from the experiment box and given more food
and its freedom in the room. This procedure could be carried
out until the chick's hunger was satisfied after which the tests
went so slowly and with such uncertainty that it was found
best to postpone the work until the following morning. As
the bird became older this mode of experimentation could be
carried on as long as three hours.

While I was preparing test sheets or taking notes at my
desk between experiments, No. 21 would crowd up about my

feet and beg to be taken up. If it were allowed to perch itself on my arm it would sit there as long as I was quiet, contentedly preening its feathers and occasionally giving a short "hovering twitter."

From these facts, I am led to conclude that the chick really "enjoyed" the experiments.

Table 7 shows the results of my first study of form with No. 21. The chick was trained to go to the triangle and to reject the circle or square. While none of the results here recorded are clear cut, there is strong evidence that the chick was discriminating between the two stimuli. This experiment was hurried lest the chick should not remain in good physical condition, but at its conclusion the bird was in excellent health so the work was repeated with much more thoroughness.

TABLE 7
Form Perception
No. 21.   Hatched: February 9, 1912.   Sex: ♀

Discrimination	Series	Date	Right	Wrong	Time
△ 28+—⊙ 7+	6	March 13	7	3	10″
" —⊙ 12+	7	" 13	9	1	11
" —⊙ 15+	8	" 14	8	2	18
" —⊙ 19+	9	" 14	4	6	12
" — "	10	" 14	6	4	8
" — "	11	" 14	8	2	33
" — "	12	" 14	8	2	12
" — "	13	" 14	8	2	12
" — "	14	" 14	8	2	12
" —⊙ 23+	15	" 14	8	2	13
" — "	16	" 15	8	2	6
" —⊙ 24+	17	" 15	8	2	13
" —⊙ 25+	18	" 15	9	1	6
" —⊙ 26+	19	" 15	6	4	17
" —⊙ 27+	20	" 15	8	2	18
" —⊙ 28+	21	" 15	7	3	17
" — "	22	" 16	9	1	8
" —□ 28+	23	" 16	9	1	40
" —⊙ 63+	24	" 18	6	4	56
" — "	25	" 18	6	4	85

The last two series (24 and 25) of table 7 were introduced as control tests. The circle was larger than the triangle, hence it afforded an opportunity to see if the chick would react to form difference, after this training, rather than size difference. Apparently it was demanding too much of the chick, for No. 21 be-

came discouraged at this point and the training had to be repeated.

In table 8 is presented the results of the re-training of No. 21. While the record, as shown in the table, is quite convincing

TABLE 8

FORM PERCEPTION: △ 28+—⊙ 28+

No. 21. Hatched: February 9, 1912. Sex: ♀

Discrimination	Series	Date	Right	Wrong	Time
△ 28+—⊙ 9+	9	March 20	10	0	6
" —⊙ 12+	10	" 20	10	0	14
" —⊙ 15+ (inscription of triangle)	11	" 21	9	1	9
" — "	12	" 21	10	0	9
" — "	13	" 21	10 ·	0	8
" — "	14	" 22	10	0	6
" —⊙ 19+	15	" 22	5	5	15
" — "	16	" 23	9	1	6
" — "	17	" 23	10	0	6
" —⊙ 23+	18	" 23	9	1	7
" — "	19	" 25	9	1	20
▽ 28+— (inverted)—⊙ 23+	20	" 25	5	5	92
△ 28+ (upright)—⊙ 23+	21	" 25	8	2	20
" "	22	" 26	10	0	17
" —⊙ 25+	23	" 26	10	0	12
" —⊙ 27+	24	" 26	8	2	12
" — "	25	" 26	9	1	6
" — "	5	" 27	8	2	35
" — "	6	" 27	6	4	8
" —⊙ 28+	7	" 27	8	2	9
" — "	8	" 28	10	0	5
" — "	9	" 28	10	0	9
△ 11+ (inscribed)—⊙ 28+	10	" 28	6	4	40
△ 28+—⊙ 28+	11	" 28	10	0	15
" — "	12	" 29	9	1	5
▽ 28+ (inverted)—⊙ 28+	13	" 29	2	5	83
△ 28+ (upright)—⊙ 28+	14	" 29	9	1	7
" "	15[1]	" 30	7	0	6
" "	16	" 30	9	1	7
" "	17	" 30	10	0	24
" "	18	April 1	10	0	15

[1] In series 15 the triangle was inverted during tests 5–7; the result was 2 wrong choices with an average time of 39 seconds.

that the chick discriminated between the triangle and the circle, it is, nevertheless, equally convincing that the chick did not perceive the form difference. It had reacted properly to the △ 28+—⊙ 19+ and —⊙ 23+ when the apex of the triangle was at the top, but when the triangle was inverted (series 20,

March 25) the animal did not choose the triangle more than half of the time. With the triangle again upright, the correct reactions returned. Proper responses were secured when the areas were equal, (series 8 and 9, March 28), but when the inscribed triangle was substituted for the standard, the chick was again confused. Series 13, (March 29), another case where the triangle was inverted, gave more decided negative results which were immediately preceded and followed by almost perfect reactions. As a further test of the effect of inverting the triangle, the inversion was made during a regular series, 15, (March 30). The result of the inversion during tests 5–7 was one right choice, out of 3 chances with an average time of 39 seconds. These three special tests were preceded and followed during the same series with *perfect* tests the time of which averaged *less than one-third* that of the special tests.

In connection with these results, I present in detail the behavior of No. 21 when it was given $\triangle$ 28+—$\odot$ 63+ discrimina-

TEST SHEET

Title of investigation, Form: $\triangle$ 28+—$\odot$ 63+
Experimented on, 21
Harvard Psychological Laboratory, March 18, 1912
Record Sheet, 2; Series, 24

Test	BEHAVIOR	Record
1 l	$/// - \overline{///} + \overline{///} \; \underset{\smile}{\bigcirc} - \overline{\overline{///}} + /// \,_{"}$	O–65
2 r	$/// + /// \,_{"}$	O–7
3 l	$/// - \bar{/} \, \bar{/} \, \bar{/} \; \triangle^1 + /// \,_{"}$	E–1–14
4 l	$/// - /// + / \, \backslash\!\backslash + /// \,_{"}$	O–14
5 l	$/// - /// \; \triangle^1 \overline{\text{/////}} + /// \,_{"}$	E–1–55
6 r	$/// - + /// \overline{\text{//////}} - /// \underset{\smile}{\bigcirc} + // - \bar{/} + \overline{//} \; \overline{\text{//////}} - \triangle^2 + \,_{"}$	E–2–171
7 r	$/// + // - // + // + \overline{\text{//////}} + // - \overline{\text{//////}} + /// \,_{"}$	O–94
8 r	$// + // \backslash\!\backslash - // \; \overline{\overline{\backslash\!\backslash}} \overline{\text{//////}} + // \,_{"}$	O–69
9 l	$/// + /// \,_{"}$	O–4
10 r	$/// - / \underset{\smile}{\bigcirc} + \overline{\overline{\backslash\!\backslash}} - / + / \overline{\text{//////}} - // \; \triangle^1 + // \,_{"}$	E–1–70

6–4–563.

tion. These tests are reported in table 7 as series 24 and 25. The test sheets show how utterly confusing to the chick was this condition. The results of this test were verified in the series recorded in table 8 under date of· March 28 where the record is the same and the behavior was very similar.

Finally this chick's response to the circle-triangle was tested. The reversion of the condition for discrimination was at first confusing to the chick, and much patience on the part of the experimenter was necessary. The plan now was to begin with

<div align="center">

TEST SHEET

</div>

Title of investigation, Form: △ 28+—⊙ 63+
Experimented on, 21
Harvard Psychological Laboratory, March 18, 1912
Record Sheet, 2; Series, 25

Test	BEHAVIOR	Record
1 r	/// + // − /// ○⎵⎵ − // + // − // ○ + /̿ ⊙̆ − / △⁰ + // ⫟	E–0–145
2 r	/// + // ⊙̆ ⁄⁄⁄⁄⁄⁄ − /// + /̿ ⊙̆ − // ○ + /// ⫟	O–79
3 r	/// + − ○ + // ⊙̆ ⁄⁄⁄⁄⁄⁄ + /// ⫟	O–45
4 r	/// ○ + /// ⊙̆ ⁄⁄⁄⁄⁄⁄ − / + /// ⁄⁄⁄⁄⁄⁄ + /// ⫟	O–60
5 l	/// ○ − // + /// − /// ⁄⁄⁄⁄⁄⁄⁄ + /// − // △¹ + /// ⫟	E–1–61
6 l	// + /// − /̿ ⊙̆ ⁄⁄⁄⁄⁄⁄⁄⁄ + /// ⫟	O–33
7 l	// + // − /// ⁄⁄⁄⁄⁄⁄⁄⁄⁄ − /// ⊙̆ − // + /// ⫟	O–46
8 l	/// + /// − ⊙̆ ⁄⁄⁄⁄⁄⁄ + / − /// △¹ + /// ⫟	E–1–35
9 r	/// − /// ○ ⁄⁄⁄⁄⁄⁄⁄ − // ⁄⁄⁄⁄⁄⁄⁄⁄⁄⁄⁄⁄ + /// ⫟	O–99
10 l	/ − /̿ ⁄⁄⁄⁄⁄⁄⁄ − △⁰ ⁄⁄⁄⁄⁄⁄⁄⁄⁄⁄⁄⁄⁄⁄⁄ − △⁰ ⁄⁄⁄⁄⁄⁄⁄⁄ − △¹ + ⫟	E–1–243

<div align="right">6–4–84.6</div>

⊙ 63+—△ 28+ and gradually to eliminate the size difference by substituting successively smaller circles. In this case the *right* stimulus area was the variable and the standard was the sign of "shock" and "no escape." From the tabulation of these results the early records are omitted since these tests were only

made as a means of getting a discrimination between the later forms. The size of the circle was gradually decreased from ⊙ 63+ to ⊙ 38+ at which point the tabulation begins. About 400 preceding tests were necessary to bring the bird to the point in its training at which the records of the table commence.

Table 9 shows that the chick was able to acquire the circle-triangle habit. The plan of controlling the qualities other than form was carried out as heretofore explained. After No. 21 had acquired the ⊙ 28+—△ 28+ reaction, the order shown in the table was followed to determine whether or not the bird

TABLE 9

FORM PERCEPTION: ⊙ 28+—△ 28+ and ⊙ 28+—□ 28+
No. 21. Hatched: February 9, 1912. Sex: ♀

Discrimination	Series	Date	Right	Wrong	Time
⊙ 38+—△ 28+	12	April 20	10	0	4
⊙ 33+— "	13	" 20	6	4	7
" — "	14	" 20	5	5	7
" — "	15	" 20	7	3	5
" — "	16	" 20	8	2	8
" — "	17	" 20	6	4	6
" — "	18	" 20	10	0	8
⊙ 28+— "	19	" 20	10	0	5
⊙ 44+— "	20	" 20	10	0	5
" —▽ 28+ (△ inverted)	21	" 20	9	1	5
⊙ 28+—△ 28+ (△ upright)	22	" 21	5	5	6
" — "	23	" 21	6	· 4	4
" — "	24	" 21	6	4	7
" — "	25	" 21	3	7	6
⊙ 33+— "	1	" 21	10	0	4
" — "	2	" 21	10	0	4
⊙ 28+— "	3	" 21	10	0	5
" —▽ 28+ (△ inverted)	4	" 21	6	4	5
⊙ 15+—△ 28+ (⊙ inscribed)	5	" 21	4	6	11
⊙ 28+— "	6	" 22	8	2	10
" — "	7	" 22	8	2	7
" — "	8	" 22	10	0	6
" — "	9	" 23	8	2	5
" — "	10	" 23	8	2	5
" — "	11	" 23	9	1	4
" — "	12	" 23	9	1	7
" — "	13	" 24	9	1	5
" — "	14	" 24	9	1	4
" —□ 28+	16	" 24	5	5	5
" — "	17	" 24	5	5	3
" — "	18	" 25	3	7	4
" — "	19	" 25	6	4	4
" — "	20	" 25	5	5	6
" — "	21	" 25	8	2	6
" — "	22	" 25	5	5	4

actually depended upon form difference. If it had a perception of form such as has been found to exist for size, then no marked change in the results should have occurred when ☉ 28+ was replaced by a circle that circumscribed or inscribed the standard triangle; and if the chick perceived three-sidedness or triangularity on the one hand and circularity on the other hand, there should have been no important modification of its reaction when the triangle was inverted.

The work on form thus indicated that the chick can discriminate between circles and triangles of equal area, and there are indications of a discrimination between circles and squares of equal area (witness series 21, April 25, table 9, and series 23, March 16, table 7), but with the application of control tests we have indications that *this discrimination is on some basis other than form*. The results from the inversion of the triangle indicate that the basis of choice depends upon the unequal stimulation of different parts of the retina. When the extended base of the triangle is so placed as to stimulate the region of the retina which was formerly stimulated by the apex of the triangle, the chick becomes confused. Under the conditions of the present experiment, therefore, I am forced to conclude that *the apparent reactions to forms are the result of keen perception of size differences*.

V. RELATIVE VALUE OF SIZE, FORM, AND BRIGHTNESS

The preceding study of size and form can leave no doubt as to their relative importance in the chick's visual life. On the basis of trial and error it has been shown that the number of tests to produce any approach towards a perfect response to the circle-triangle is vastly greater than the necessary number in the case of the large-small discrimination. This study has also revealed the fact that even after perfect reactions to the circle-triangle were established, the form element played no part in the discrimination. The size element, under these conditions, is *the* important factor for the chick, and *form in the stricter sense* has been found to have no discriminative value.

A brief study was made to determine experimentally the relative importance of size, form, brightness, and general illumination. The subjects used were Nos. 15, 16, 17, 18, 20, and 21. They were trained to go to a triangle which had a greater

area and was brighter than the simultaneously presented circle. The triangle also appeared in the compartment which was more highly illuminated than that in which the circle was presented. After the chick had learned to choose the triangle without any errors, all but one of these factors were eliminated. It was thus determined which factor had the greatest value for the chick.

This method, I clearly recognize, is not reliable. It was only adopted as a means of securing preliminary information on this particular problem. The most important defect which may be present is that it provides no certain way of ascertaining the threshold values for each visual factor. For example, a difference of 11 sq. cm. between the areas of the two stimuli may be high above the chick's threshold of difference, whereas the difference between a triangle and a circle may be scarcely above this liminal threshold. I had no way of equalizing the four factors for discrimination. Subsequent work such as that reported on size and form must determine these values for all of the "light" elements on the basis of right and wrong choices.

The amount of difference in brightness and general illumination was that which, under the mechanical conditions previously described, would result when the *right* source lamp was placed 125 cm. from its stimulus area and the *wrong* lamp was 240 cm. from its display surface. This caused a marked difference to the human eye both in brightness and general illumination. Table 10, however, shows that it was of little significance to the chick. According to the averages, size was the first factor; *right* choices depending upon it alone amounted to 86%. Brightness and general illumination combined stand next with nearly 70% of *right* choices, and form stands last with the *right* and *wrong* choices nearly equal. Considering these results in connection with those previuosly presented on size and form, it seems highly evident that *the relative values of light factors for the chick's vision is respectively size, brightness and general illumination, and form.*

VI. GENERAL IDEA

The frequent recurrence of discussions relative to the general idea in connection with animal studies has had the effect of keeping before me, during the present study, the question whether or not the chick has a general idea of sizes and forms. Accordingly, after several subjects had been trained to make

TABLE 10
Relative Values of Visual Factors

Condition of Discrimination	Series	Date	Subjects																		Average		
			15			16			17			18			20			21					
			R	W	T	R	W	T	R	W	T	R	W	T	R	W	T	R	W	T	R	W	T
△ 28+ brighter and in lighter compartment than ⊙ 7+ .	1	Feb. 20	10	0	34	8	2	40	9	1	16	8	2	40	7	3	40	9	1	10	8½	1½	30
	2	22	10	0	8	8	2	10	9	1	10	10	0	5	7	3	33	9	1	18	8⅝	1⅛	14
	3	24	9	1	8	8	2	21	10	0	7	10	0	8	8	2	12	10	0	5	9	1	10⅛
	4	26	10	0	3	6	4	35	10	0	6	9	1	4	9	1	10	10	0	3	9	1	10⅛
	5	27	8	2	11	7	3	24	9	1	22	7	3	16	9	1	21	6	4	12	7⅔	2⅓	17⅔
	6	28	9	1	7	9	1	7	10	0	6	10	0	4	10	0	7	10	0	3	9⅔	⅓	5⅔
	7	29	9	1	14	9	1	4	10	0	5	9	1	6	10	0	8	10	0	2	9½	½	6½
	8	29	10	0	3	9	1	9				10	0	2							9⅔	⅓	4⅔
	9	Mar. 1	10	0	5	10	0	20				10	0	7							10	0	10⅔
	10	1				10	0	12													10	0	12
Form and size......	11	1-2	8	2	8	9	1	22	6	4	4	8	2	10	10	0	4	9	1	2	8⅓	1⅔	8⅔
Form............	12	2	3	3	—	3	3	—	3	3	—	2	4	—	4	2	—	4	2	—	3⅓	2⅝	—
All factors combined	13	4	10	0	6	9	1	45	10	0	4	7	3	36	10	0	4	10	0	3	9⅓	⅔	16⅓
Size.............	14	4	9	1	7	9	1	30	10	0	3	8	2	4	9	1	3	7	3	6	8⅔	1⅓	8⅝
Brightness and general illumination .	15	5	5	5	9	6	4	26	9	1	5	7	3	3	7	3	7	7	3	5	6⅝	3⅛	9⅔

perfect reactions to the condition ⊙ 28+—⊙ 12+, I tested, without further training, their reactions to two different circles the sizes of which bore the same relation to each other as that of the former pair. This test was made for two different pairs of circles to determine whether or not a chick trained to choose the larger of two stimuli will choose the larger of two other stimuli that are larger or smaller than, but have the same proportion in size as those with which it was originally trained.

The diameters of the circles used in ⊙ 28+—⊙ 12+ discrimination are respectively 6 cm. and 4 cm. The variable, therefore, is two-thirds of the standard. After the chick had reacted perfectly to the 6-4 circles, they were replaced with two circles having diameters respectively of 4 cm. and 3 cm., *i.e.*, having the same difference ratio. In the next place they were replaced with two 9-6 circles in which case the difference ratio again remained unchanged. All of the subjects, except No. 3, mentioned in the foregoing discussion, were tested in this manner.

The results of these tests for general ideas are briefly as follows: a chick which has been trained to choose a 6 cm. circle and *reject* a 4 cm. circle will *choose* the latter when presented with a 3 cm. circle. Likewise, it will choose a 9 cm. circle when presented with a 6 cm. circle. In the one case, what has formerly been the sign for a negative reaction is accepted as the sign for a positive reaction. In the other case, what has previously been the positive sign is rejected, when presented with a larger stimulus, as a "shock sign."

VII. SUMMARY

Under the conditions of the present method, the chick's threshold of difference in size perception lies between one-fourth and one-sixth when the diameter of the standard circle is 6 cm.

Earlier experimenters on the chick's perception of forms have failed to eliminate all possible conditions for discrimination other than the factor of form. The chick can discriminate between circles and triangles and circles and squares which are equal in area, but, with the conditions as described in this paper, none of the subjects with which the present experiment has been conducted were able to discriminate between visual stimuli on the basis of form alone. Reactions to optical stimuli which have been interpreted by observers as indicating form discrimination are probably made on the basis of unequal stimulation of different parts of the retina. If local inequality of excitations on the retina be the basis of these reactions, then the apparent discrimination of form by the chick is, in reality, a keen perception of size differences.

In sharp contrasts with the reactions to form stimuli are the responses to sizes. A chick can acquire a perfect circle-triangle reaction, but control tests show that it has no general idea of circularity in contrast with triangularity. On the other hand, a "large-small" trained chick reacts positively to the larger of two stimuli even though this particular stimulus had been the "shock" stimulus in previous experiments.

The order of importance of factors in the chick's vision is size, brightness and general illumination, and form.

NOTES ON THE DEVELOPMENT OF A YOUNG MONKEY

K. S. LASHLEY AND JOHN B. WATSON

From the Psychological Laboratory of The Johns Hopkins University

Seven Plates

Since some interest attaches to the development of the young of any species of animal on account of its bearing upon the control of experimentation in behavior work, it seems worth while to present the diary given below of the growth of a young *Macacus rhesus* monkey. The diary affords some rather interesting points of comparison between the development of the human infant and the young monkey. While comparisons can not be closely drawn it may be said at the outset that the difference in the motor and sensory preparation of the two species of young at birth is enormous and that the more rapid course of development in the young monkey is still more remarkable. We were not at all prepared to find the absence of a prolonged period of infancy in the monkey. That this is the case is apparent from our notes.

The two male monkeys in the Johns Hopkins Laboratory were purchased at Chicago in 1904-1905. The older monkey, Jimmie, was probably at the time of purchase three years old, and the second, Billy, about one year of age. The female, Dolly, was purchased in Baltimore in 1907. She was probably three years old at purchase. Their ages now are (J) eleven, (B) eight, and (D) eight respectively. Until 1911 the monkeys lived together at various times in the ordinary large laboratory cages. A change was then made so as to give the animals greater freedom. A yard was fenced in which connected by a chute (12″ x 12″) with a steam heated room. The animals could spend their time at will either in the yard or in the room. Even in the coldest weather a large part of their time was spent in the open yard.

During the three or four years prior to this change in their living arrangements copulation between J. and D. took place frequently but there was never any evidence of conception resulting. We were accordingly not expecting the birth of the

young monkey nor did the female show, even up to the time of parturition, any signs of pregnancy which could be noted by external cursory examination. The time of gestation is therefore not determined.

Since we desired to keep the young monkey in good health no attempt was made to separate it from its mother. For this reason the notes are rather superficial—such as could be obtained by watching the animal's activities in the open yard.

July 11, 1912. First week.

The young monkey, a male, was born between 9 and 10 A. M. First observation at 1 P. M. The mother (Dolly) was sitting on the shelf,[1] crouched on her haunches and bent over. She supported the baby between her thighs, one of her hands about his back, the other (left) about his shoulders with the fingers passing under his left arm. The baby sits breast to breast with the mother, his right hand on her left shoulder, his left grasping the hair of her right side. His hind feet grasp the hair just above her hips. He nurses from the left breast. This seems to be the typical position for both in resting and sleeping.

When moving about Dolly carries him suspended under her breast, with one hand, usually the right, grasping his neck and holding him against her. Her other hand is used in walking and feeding. The baby grasps the hair of her sides with all four paws, his legs straight and extended up along her sides as far as they will reach. His eyes are closed and his face pressed tightly against her breast. He looses hold with his hind feet. Dolly stops and presses tightly against his neck. He kicks about and finally regains his hold.

Dolly objects to the presence of observers, watches us, and finally starts to go inside through the chute. At the passage she hesitates as though to make sure that her own body and that of the baby will go in. She holds him very tightly on entering.

6.00 P. M. Found them seated on the shelf in the usual position. Dolly catches the baby by the fore-lock and stretches the skin of his forehead tightly back, gazing intently at his face. She then fingers his eyes, nose and mouth. She grasps his right

---

[1] The shelf is six feet from the ground and is eight feet long by ten inches wide. Ascent is made by a long, narrow, inclined plane.

ear and pulls his head over to one side, looking for fleas. The
baby cried out, a high-pitched, metallic squeak like that of a
rat. The mother clasps him tightly for a moment in both hands,
then resumes her search for fleas. The baby grows restless,
stops nursing, and moves his head about, his eyes open. He
is not able to hold or turn his head steadily.

6.15 P. M. The baby sits on the ground, still clasped in the
mother's arms. His thighs are drawn up until the knees are
almost even with his spine.

6.30 P. M. Dolly carries him constantly and keeps her back
turned towards us most of the time.

6.40 P. M. Found her seated on the edge of the water bucket,
a large galvanized garbage pail, trying to drink. When she
stoops over the baby is in danger of dipping in the water. She
makes several unsuccessful attempts to drink, but finally gives
up and goes to the shelf. She almost immediately settled down
for the night. Both went to sleep in about the position de-
scribed before.

We were not able to disturb the baby by shrill whistling or
to get him to attend to movement. The times when he looked
around were very short, only a few seconds, and his eyes did
not seem to be directed toward any particular object.

July 12. 7.00 A. M. Both were found still in the sleeping
position. Dolly spends 10 or 15 minutes looking for fleas, then
climbs down from the shelf and comes to the gate. She leaves
the baby to cling fast by himself, instead of supporting him
with her hand as she did yesterday. He holds with all four
paws, one around her left foreleg. When he looses hold, as he
frequently does, she lifts him back into place but does not sup-
port him there.

The baby seemed restless when one whistled within a foot
of his ear, moved his head about, and finally looked around
indefinitely, but did not appear to localize the sound. He
would not follow a moving object with his eyes.

Dolly offered herself to Jim, the large male in the yard and
father of the baby, for copulation, resting the baby on the
ground and crouching over him.

5.00 P. M. Found her lying stretched out in the position of
a sleeping cat, with the baby resting on the ground against her
breast.

July 13. 12.00 N. The baby is stronger and holds to Dolly without slipping. He holds up his head more steadily and gazes about for half a minute at a time. He is much troubled by a cold. We offered Dolly bread and milk and when she took it, Jim, wanting it all, attacked her savagely. She did not fight back as usual but screamed and fled to the shelf. She seems weak today, rests the baby on the ground instead of holding him upright, for much of the time, and leans, herself, against the incline to the shelf. As she sits ordinarily her body offers a perfect protection for the baby. Her thighs protect his sides and her body is bent forward to form a roof, so that only the top of his head is exposed. She usually turns her back to the observer, keeping the baby hidden and glancing back over her shoulder.

My moving hand caught the baby's attention today. He opened his eyes wider and turned toward it. Later he turned his head to follow movements and, when his head was confined by Dolly's arm, turned his eyes. He does not yet attend to sounds, but this is not surprising on account of the constant racket made by terns confined in an adjoining yard.

7.00 P. M. The young one is lying on his back, his hind feet grasping the hair of Dolly's sides. He moves his hands about in an aimless way, grasping at her face. His movements are weak and inaccurate. Dolly licked his face for a few seconds. This is the only sign of cleaning that has been observed.[2]

Frequently in her flea hunting she is too rough and the baby cries. His cry has changed to a shrill chattering, "Chirk-chirk-chirk."

7.30 P. M. The monkeys are preparing for the night. Jim stretched out on the shelf and when Dolly edged over to him he drove her down to the ground. He has been growling at her all day.

July 14. It rained all afternoon and Dolly would not leave the shelf. Both she and the baby remained almost motionless all afternoon.

July 15. The baby is much more active today and spends much of the time looking around. He rides with his head turned away from Dolly. He shows especial interest in Jim,

---

[2] From later observations it appears that this is only a method of catching fleas. Dolly has never attempted to wash or clean the baby.

staring at him when he is close and moving, but not following him when he moves out of the direct line of vision. He twice reached out towards Jim, with a quick out-thrusting of the arm, followed by a sweeping movement. Usually the movements of the arms are restless and not directed towards any object. The thumb and fingers of his foot seem to be more readily apposable than they are in the adults.

When sitting on the shelf Dolly does not hold him so closely as before, but allows him to lean back until he lies flat on his back.

Jim is becoming more abusive and does not allow Dolly to come near him.

July 16. The caretaker reports that as Dolly climbed down from one of the flying rings the baby scrambled around to her back and remained there until she reached the shelf, when he returned to his usual position. The baby is more active today than yesterday. He holds his head up steadily and gazes about; moves his arms about and fumbles at his mother's arms and shoulders.

2.00 P. M. Jim attacked Dolly savagely and we were forced to place Billy, another male monkey, and him, in the winter room adjoining Dolly's yard. When the separation of the monkeys was attempted all were badly frightened and Dolly tore about the cage, leaping to the sides and roof and finally dropping from the roof to the ground. The caretaker stood before the connecting chute after Jim and Billy had entered and Dolly rushed against him violently enough to bruise him severely. At some time, probably when Dolly leaped down from the roof, the baby received a cut above the left eye and a bruise on his right hand. Nevertheless he clung tightly to Dolly without her help during the whole commotion. He cried out only once, when she leaped from the roof.

As soon as the chute was closed Dolly became quiet, but went to the window and peered in several times. The baby held tightly to her, with his face close to her breast, for the remainder of the afternoon.

July 17. The baby is very quiet today and seldom turns his face away from Dolly. He sneezes frequently and always cries afterwards. When he cries Dolly gathers him to her closely.

I was not able to attract his attention by any noises, but when, rarely, he looked around he was attracted by my moving hand, and followed its movements with his eyes.

July 19.   Second week.

In catching fleas Dolly frequently pinches the baby with her lips, making him squeal.   When he cries she pauses in her flea catching and draws him close, then licks her lips and looks at the sky.   In half a minute she is at it again, turning back the hair from his skin and going over him from his nose to the tip of his tail.

In nursing, the baby bites her nipples until he makes her shudder.   When he does this she generally looks down at him, then stands up and walks about.

He is beginning to show an interest in objects other than his mother.   As she walks along he holds fast by three feet, and swings the other free, reaching toward the ground.   He looks around actively all the time when not feeding.   When Dolly is still he moves about restlessly in her arms, releases his hold on her fur, and rises slightly on his hind feet.

July 20.   Today the baby tried to escape from Dolly's arms, twisting about and kicking violently.   These movements did not seem to be purposive but were rather an undirected, violent squirming.   He bites at Dolly's arms and his own hands.   When he bit her teat today she first tried pushing his head about with her hands and when this did not make him quit, she pinched him on the shoulder with her lips.   This made him chatter, when she immediately gathered him close.   When Dolly walked her moving hand caught his attention and he snatched at it, tripping her.   She pressed him up firmly into position and went on.   This was repeated several times.

When looking at me he sometimes purses his lips and thrusts out his tongue and sometimes reaches towards me.   Most of his movements are of the larger limb muscles; the fingers are not moved separately.   He does not imitate any of Dolly's movements.

July 22.   He is beginning to give Dolly trouble to hold him. As soon as she sits down he struggles to escape, reaching over her arm to the ground with his hands, then kicking out his feet.

At other times he tries to creep under her arm, but does not attempt to push it aside with his hands. Once he succeeded in throwing himself forward over her arm and stood alone. She caught him by one leg and pulled him back, then put her other hand around his neck and drew him into place.

He gives a scratching reaction today for the first time. The hind foot alone is used, scraping clumsily at his back and head. The movements are slow and uncertain.

He has grasped at several objects but does not pick them up, and he reaches out toward his mother's hands when she moves them. He frequently puts his hands in his mouth, especially fater he has scraped them along the ground, or has grasped at some object.

Some of his movements indicate a lack of distance perception. Gazing intently at some object (carrot) he throws himself violently forward over Dolly's arm, at the same time reaching out with both hands, as though in an attempt to grasp it, although it is as much as three feet away.

While he was facing away from her Dolly became frightened. She leaped to her feet, grasping him around the throat, and started to run away. When he cried out she stopped, looked down at him, then grasped him by one hind leg, turned him over into position, and ran on.

He now turns directly towards the source of sounds and follows movements accurately with his head. He attends much longer than at first, looking at the observer as long as half a minute at a time. Unlike the adults, he meets the eye readily. He would not reach toward a moving hand or a stick thrust into the cage.

July 23. The caretaker reports that the baby was out of Dolly's arms and walking for the first time at 10.00 A. M. today. At 1.30 Dolly climbed up on the gate. The baby dropped down between her thighs and hung by one hand for a few moments. When she is walking he clings to her tightly but the moment she stops he tries to escape. I gave Dolly a bit of chocolate. While she was eating it, the baby began to creep away. She put out a hand to stop him, thought better of it, and walked away a couple of feet, looking back at him. He began to crawl after her but his hind legs were too weak and he fell over. As he approached Dolly moved farther away, and

finally the baby gave up and, turning aside, began to chatter. Dolly immediately came to him and picked him up. Five minutes later he escaped again. Dolly moved away from him about four feet and stopped, waiting for him to follow. He advanced a few steps then squatted down and looked around. Dolly immediately ran to the window and looked through at Jim, making threats. Baby turned toward the wall and began to chatter. Dolly became excited, ran from one window to the other, growling and barking. The baby became very much frightened, chattering continuously, and Dolly finally ran to him, picked him up, turned him over while running, and climbed to the shelf.

July 24. It rained almost all day and Dolly remained in the sleeping box on the shelf. I could not coax her out. The baby kept close to her and did not try to escape.

July 25. Third week. •

Today for the first time I saw the baby use his hand effectively. While watching me, he grasped Dolly's left nipple with his right hand and carried it to his mouth. The movement was quick and accurate, quite different from his usual vague clawings.

He walks better today, having gained some control of his hind legs. He even managed a shambling trot for a few steps until one of his feet was misplaced, thus upsetting him. He shows little fear when left alone but watches his mother closely and keeps near her. He was out of her arms for about 15 minutes during the three hours that I watched. Squatting in front of the wall, he suddenly throws his body forward and thrusts his hands against it, at the same time pursing his lips and drawing up the corners of his mouth. This is repeated frequently and seems to be the first definite attempt at play.

Baby followed Dolly for about 15 feet. When she stopped and sat down he climbed against her back and began to muzzle about as though seeking her teat. She reached around, caught him by the neck and pulled him into position.

July 26. Baby was not on the ground during the time that the observer was present. He spent all the time in nursing or sleeping. A day of great activity seems to be followed by one of depression or exhaustion.

July 27. Today the baby is very active again, never still a moment, even when feeding. While on the ground he grasped a piece of paper, pulling it back and forth from one hand to the other. He finally dropped it and put his hands in his mouth. He bites at everything within reach; probably cutting teeth. He walks well although his hind legs are still weak. He tries to climb to Dolly's shoulders but is not strong enough to lift himself.

He sits in front of Dolly, facing her, then rises on his hind feet and thrusts out his hands against her. This is repeated frequently. Once he fell over backwards. Dolly was excited, ran to him, snatched him up and fled to the shelf.

While he was on the ground she climbed up to the shelf, stopping three times and looking back at him, as though coaxing him to follow. He put his hands upon the incline, but did not attempt to climb up. After a short time he began to cry and Dolly came down to him immediately.

When he is on the ground one cannot make the slightest movement without bringing Dolly to him, even when she has seemed to be looking the other way.

He found the wire on the water bucket. Grasping it with both hands he attempted to climb up, placing his feet against the side of the bucket. He could not lift himself. While Dolly was looking in at the window he fell down and gave a faint cry of fright. Dolly turned, reached him in two leaps, picked him up, chattered at me, and fled to the shelf.

August 1.   Fourth week.

No new activities have developed during the last three days. Feeding has caused Dolly to lose her fear of me. She allows the baby to come quite near me, and only threatens when I move.

When he is on the ground he watches my movements almost constantly, coming up as close to me as he can and standing up against the screen. His movements, reaching, grasping, scratching, etc., are not very accurate. In grasping the thumb is not apposed to the fingers, but the hand is used as a sort of scoop, as is that of a raccoon. While he was near the netting I thrust my finger through to him. He nosed about and bit the

finger, exposing his toothless lower jaw. After sucking at the finger he drew back with a frown.

His face is not mobile but he has three easily recognized expressions; ordinarily his face is impassive, with an expression of great seriousness, even melancholia; when he is satisfied or interested he sucks his tongue, pursing up his lips and chewing; when angry or disappointed he frowns. There is no expression comparable to the human smile.

He is quite unafraid and is attracted only by the observer's movements. He is frightened by squeaking or tearing sounds,[3] but not by whistling or clapping. He runs about actively and bites at every new object.

August 3. Baby climbed some distance up the wire netting today. When he was 18 inches from the ground Dolly reached up and pulled him down into her arms. He seems to enjoy climbing up and down the edge of the window sill, a distance of about four inches.

I put a bit of bread and milk in his mouth. He sucked at it but did not attempt to swallow it, finally letting it fall from his mouth.

He has learned to jump from the window ledge to the ground. Previously he would put his hands to the ground before dropping off; but now he drops boldly.

He tastes the bread and milk that I have given Dolly, usually placing his hands upon it and bending down to suck at it. Twice, however, he gathered a large piece of bread up into his arms, sitting back upon his haunches. The hands are not used well for grasping. He does not try to swallow the bread, but merely sucks at it. His biting seems now to be limited to light colored objects, bread, paper, carrot, etc. When Dolly is feeding and he approaches her she crouches down until her face is level with his, stares at him for a moment, then slaps or bites him. This makes him cry and she immediately draws him into position.

August 7. He is very playful today. He stands up on his hind feet, runs forward a few steps with arms outstretched, and pounces upon a piece of paper or other object. He climbs

---

[3] Noises of this type, rustling, tearing and squeaking sounds, seem to be particularly terrifying to the young of animals differing widely in habit.

about the edge and sides of the water bucket. He does not seem to mind when his feet or tail get in the water. He reaches out, grasps and bites his food. His interest in the food is quite independent of Dolly's activities. He does not imitate her in eating or in other movements. She has never offered him food, —indeed she usually snatches it away from him and boxes him besides.

His scratching reaction is complete today. The hind foot is moved quickly and accurately. The hand is used for scratching for the first time. The movements are exactly those of the adults. The wrist is held stiff and bent slightly inward, the fingers crooked. Even the adult's far-away look is assumed during the process.

August 8 and 9. Fifth week.

Cold rain. The baby was reluctant to leave Dolly's arms and would not venture far from her. He climbed up on the netting and some cake crumbs were placed in his mouth. He sucked at them but did not swallow.

August 10. He has cut lower incisors; tried to test his taste sensations today. He took sugar and acid solutions with apparent relish, coming back for more, but he turned away when salt was given. He ate bread and milk with apparent liking. When the observer quit feeding him he climbed up on the screen and, looking at him intently, he began to shake the screen, or rather, to bounce back and forth against it, since his weight was not sufficient to move the wire. He struck at Dolly when she pulled him down from the screen and was severely punished for it. She does not allow him to make threatening movements towards her, and she frequently bites him when he frowns at her.

August 12. Today baby apposed the thumb and fingers in grasping (first time actually observed). He could not pick up a grain of corn in this way. He frequently jumps off the window ledge and sometimes jumps into the air when running on the ground. He pounces upon various objects in the cage, but rarely picks them up, usually bending down and applying his mouth to them. He frowns very darkly when Dolly punishes him. When he is frightened he turns directly to her. When a

piece of paper was crackled he looked back and forth from her to the observer, and finally began to cry.[4]

August 14. Attempted to test his sense of smell today. When he was offered anything through the screen he reached for it with one hand, then bent forward and took it in his mouth. He sometimes seemed to smell at it, but that this is not the case was shown by his biting at a cloth wet with ammonia. Only after two attempts to bite the cloth did he show signs of displeasure at the odor. He drew back also from a cloth wet with chloroform, shaking his head from side to side and wrinkling his nose. He seemed indifferent to the odor of oil of cloves or acetic acid. Dolly now releases him on the shelf but does not leave him alone there. She watches him closely to see that he does not fall off.

August 16. Sixth week.

He is beginning to recognize food, apparently, for his biting is limited almost entirely to scraps of food scattered about the cage. He chews and swallows bread.

August 18. His interest in food is increased and he spends much of the time nibbling at scraps. His interest in our movements is decreasing, and we cannot coax him to the screen as readily as before.

He climbed up the screen and, holding with his hands, began to dance against it with his feet (the shaking reaction shown by Jim). He kept his eyes fixed upon us all the time and stopped occasionally to peer through the wire, as though expecting some response to his action.

The water bucket offers a good place for climbing, and he frequently scrambles over it, turning and twisting about, hanging upside down, and reaching accurately for the wires and edge of the bucket.

When Dolly slaps him he shuts his eyes tightly.

August 19. Dolly was sitting on the edge of the bucket and he was hanging to the screen opposite her. Letting go of the

---

[4] This is an action that has been frequently noted in the adults. When Dolly becomes enraged at some act of the observer, she does not herself attack but turns to Jim, the large male, and induces him to take the offensive. The behavior of the baby resembled this action of hers very closely.

screen with his hands, he turned and sprang across the bucket, striking against her breast and catching at her shoulders. His hind feet dropped into the water, but Dolly caught him and drew him up into position.

August 20. I pinched his toes when he had climbed up on the screen. He scrambled away and when I quit he gave a slight shaking reaction, dancing up and down against the screen.

August 21. Dolly left him alone on the shelf while she came down to eat. He began to cry as soon as she had left him, but made no attempt to get down. After a few moments Dolly climbed back to the shelf and carried him down.

His grasping is now almost wholly with the thumb apposed, and he is able to pick up small objects such as broken grains of corn.

August 26.   Seventh week.

Baby is beginning to notice his own body. Up till now he has occasionally caught hold of his feet, but has never looked at them while holding them. Today he caught hold of his toes and looked at them carefully, spreading them apart with his fingers. He caught the skin of his breast, spreading it out, examining it for a long time. Other parts of his body were also explored. He picks at Dolly's body too, especially at her right nipple and at her chin.

When we took the camera into the cage he was quite unafraid and persisted in coming close after the camera was focused.

I dropped a bit of bread through the screen to him. He lost sight of it and commenced to scratch around as though looking for it. However, as he has never been attracted by food when it fell near him, it is possible that this activity may not have been related to the sight of the bread.

August 27. Baby is jumping today to a much greater extent than usual. He runs and springs up into the window ledge. He also leaps against the water bucket and springs up and catches its top (about 18″ in height). The movements involved here are not different from those in his earlier play activities, but the energy expended is now sufficient to lift him from the ground. From general observations I had gained the idea that

he is somewhat left-handed. Today, however, he grasped first at various objects 17 times with the right hand and 13 times with the left. Later, more extensive observations show that he is practically ambidextrous.

August 31.   Eighth week.

Monkeys were fed green corn on the cob and syrup soaked rolls. They are especially fond of the latter. The mother immediately took possession of the rolls, after husking the corn. She carried both to the shelf. She forced the young monkey out of her arms. He began to eat in a half-hearted way at the corn but tired of it and approached the mother and reached out for the rolls. This led to severe and continued chastisement. She first pulled him away, holding him on level with her eye, and looking fiercely at him all the while. Then cuffed him with the paw, and bit him upon the skin of the head and back. The young monkey was forced to keep out of her reach. He became very angry, chattered and hopped up and down in one place, which seems to be the simian infantile way of expressing anger. He left the mother for the whole length of the plank and concealed himself behind the sleeping box. When I made noises designed to frighten them she would go over to the young monkey and place him in position but would not allow him to nurse. She will not allow him to touch food which she is holding in her hands. The forcing away of the young monkey and her increasing unconcern about him lead us to believe that this is about the time that weaning begins under natural conditions and at this age (seven weeks) he might easily be removed from the mother.

September 2. The young monkey is in a very playful mood. Spent nearly an hour out of mother's arms. Practiced jumping and climbing most of the time. Co-ordination much more advanced. Began climbing up about two feet on the wire netting, then turning with back to wire and jumping two feet into yard. Did this several times. Began new set of play movements; climbed up 18″ to 20″ and then turned back to netting, held on with right hand and slowly put left up over shoulder and back until he caught the wire and remained in that position for several moments. He seemed to get a good bit of fun out of this for he did it several times. Would crumple

up a piece of paper and spring up and back from it again and
again. Tried to interest mother in the game. Struck at her
with left fore foot and then sprang on paper and partially rolled
over on it much as a kitten does. Picked up a piece of roll
from yard with fore paw and put to mouth and bit off small
piece, reached up with left hind foot and grasped it much as
the adults do. Came to opening and bit off piece of banana,
chewed it with effort and swallowed some of it. Caught clear
view of mouth. Both upper and lower incisors are cut and
evenly grown but no molars either in upper or lower jaw.

No sign of sex interest even in play. Seems never to be
interested in sex organs. Yesterday mother went over him for
nearly half an hour, carefully picking over sex organs. No
evidence of tumescence or of movements indicative of sex
impulses.

Was very venturesome in climbing today. Climbed up the
sides of the fence for three feet—came down, then went to top
of fence and climbed with body inverted along top of fence.
Got frightened. Twice essayed to get back to sides of fence,
hanging suspended with three feet while groping for sides of
fence with other. Although he could easily make it he could
not gather courage to release the three feet attached to the
overhead netting. Finally cried and mother climbed up, grasped
him by back of neck and easily pulled him into position. These
release movements of digits do not seem well co-ordinated.
Often in attempting to climb down from netting the toes and
fingers fail to release promptly.

September 5. Noticed use of cheek pouches for first time.
Was eating rolls, and apparently with relish began stuffing into
pouch with all the vigor of an adult.

September 7. Ninth week.

Eating much larger quantities of food but still nursing as
vigorously as ever from mother. Ate almost a quarter of a
banana. Gave it in small quantities from my finger. Had
good opportunity to investigate teeth. No appearance yet of
molars. For the first time he used fingers almost exclusively
for picking up food. Picking up small bits nearly everywhere.
Hitherto his grasp has been insecure. Still there is a long latent
period both in closing and in releasing. Shown when I gave

grain.   Picked up large handfuls, letting most of it slip to ground.   Usually managed to get one sun-flower seed into his mouth, "gummed" it round and round but did not crack hull.

September 9.   Uses pouch freely, using back of forefinger as do adults for forcing food into mouth.   Mother left him more freely than ever before.   Uses the humped up, slow "lope" of adult.   Covers ground rapidly.   Enormous strides within last two days in motor development.   Sure of his leaps and does not over-innervate and lose control.   Today for first time left mother and ran up inclined plane almost to top.   Could not get over edge.   Mother paid no attention to him but ran on up incline and sat on shelf.   After three or four efforts youngster clambered over and sat on shelf.   Mother left him to clamber down for food.   Played on shelf for half an hour.   Mother lay down, fore-feet out like sleeping cat.   Baby played leap-frog over her back, running the whole length of the shelf.   At times would stop, sit on haunches, throwing up one hind-foot and slapping it with fore-foot.   These movements were all of the relaxed and infantile type.   They seemed to be a part of the play.   Indeed, in all of his play movements there seem to be as many of the non-adaptive type as of the adaptive.   Those multitudinous functions which are to be of use in the adult seem to gain in accuracy only by being exercised in the act for which they were intended, i.e., are slowly learned as they are called for.

Within the past week all of the vocal sounds of the adult have been heard with the exception of the ones which are used in the exercise of the sexual function.   They are in a high falsetto key.   Many of the adult expressive (emotional) movements are present.   On viewing Billy through fence (Sept. 5) he began bouncing on fence with hind legs holding on by fore legs.   Rotated skin of forehead and scalp up and down as he gazed fixedly at Billy and exchanged similar sounds with him.   This type of behavior is like that exhibited by two adult strange monkeys placed in adjoining cages.

Even during this past week when the young monkey has begun showing independence the rigorous vigilance of the mother is never relaxed.   She springs to him upon the occasion of any alarming sound or strange or sudden movement of the experimenter.   She is growing more resentful of any liberties with her food.

September 10.   Up to today signs of sex activity or interest have been lacking.   Today erection appeared.   Mother had fed, and had carried baby to the shelf.   He was restless and danced about trying to get down.   She tried to nurse him three or four times but he always struggled to free himself.   Finally she held on tightly to him and began to pick him around the sex organs.   Erection appeared.   The mother continued to pull at organ and to push back fore-skin.   Baby became very quiet and began to nurse, pulling at the short rope attached to her collar with one hand and reaching back to play with his own sexual organs.   I have seen the mother pick over his sexual organs often before but this never before produced an erection. Apparently the testicles have not yet descended.   They are plainly apparent, being lodged about two inches from the end of the scrotum.   Whether there is any actual descension or merely downward growth from this point is not easy to say.

September 12.   Baby very active.   Mother at first would not come down for food.   Young monkey made several tentative efforts.   Finally mother came down without him leaving him upon the shelf.   He was frantic and cried and danced in rage. She paid not the slightest attention to him and even when she went back she did not take him up or allow him to nurse.   He was very eager to eat of her milk soaked bread but dared not reach for it.   He made several playful strikes, rearing up on hind legs and striking with fore feet.   Several times when he attempted to nurse she pulled him away and put her head down on a level with his and frowned in his face.   We have here another step in the process of separation between the two.

September 12–18.   Tenth week.

Eyes, which were deep blue at first, have changed into brown, characteristic of species.   No evidence yet of cutting of molars. Seems to be slow period of development.

October 21, 22, 23.   Fifteenth week.

For several weeks development of new responses has been slow.   The monkey has been in the best of health and growth is apparently normal.

On the above dates it was noted that the young monkey was able to run down and up the inclined plane very readily.   Long

leaps and bold springs were taken. The mother came down quite often for food without him and often ran back carrying food but leaving young one behind. On the 21st he attempted to carry up his own food, a large piece of bread, in his paws. Dropped it when he started to climb. Went back for it and carried it up in mouth. Slides down the inclined plane as the fireman his pole. If he drops food from shelf or if mother drops food when he is without he runs down and takes it up. Now has a favorite place for eating, a beam resting about half way between ground and the shelf. Mother is now fairly independent. She knocks him around much as she would a smaller adult. Young one still nurses. As a rule she still carries him down. The protective instinct is still strong. Any noise or threatening movement will make her grasp him as of old.

The canine teeth are now well out. The molars are beginning to appear. Eating is evidently somewhat painful. He can eat only the softest food still. Peanuts, grain, sunflower seed, etc., are hardly touched. Milk soaked bread, soft baker's bread, bananas and grapes are all eaten with relish. He attacks the sweet potato and the carrot but makes no headway. Within the last fortnight control of hands is greatly improved, picking up tiny bits of food from between cracks, and small bits of banana from the wires. On the 22nd he peered underneath side of cage and caught sight of a brass padlock lying at my feet. Reached arm underneath and tried to pull lock forward. Mother immediately came up and peered through crack, drove young one away and tried on her part to draw lock forward. This type of imitation is evidently common in these animals.

From this period up to December 16th there has been very little to record. Due to the onset of cold weather all of the monkeys were again placed together. This made conditions rather unnatural because of Jimmie's continued cruelty. After a few days he had to be removed. The mother carries the baby constantly while in the enclosure with the other monkeys. The young one in his turn seems in constant fear of his life, rarely even attempting to get away from his mother. There are two more steps in the development which we would like to obtain— the age at which the mother entirely weans the young and the age at which sexual maturity is reached. Since under the present living arrangements of the monkeys these two obser-

vations are hard to obtain, we have decided to present the work as it stands.

The most complete as well as the earliest published observations upon the young of this species are those of Cuvier. The original publication has not been available but Brehm quotes from it in full, and for purposes of comparison it has seemed best to repeat his quotation here.[5]

"Immediately after birth the young Bunder (*M. rhesus*) clasped himself to his mother's breast, holding to her hair with all four hands and seizing her nipple in his mouth. For fourteen days he did not leave his mother's breast. He remained, always in the same position, always ready to suckle; sleeping when the adult sits down, yet clinging fast to her even in sleep. He released one nipple only when he wished to grasp the other, and so the first days of his life passed without his having made a single movement except those of the lips, to suck, and of the eyes, to look about. Like all apes he was born with open eyes, and it seems that from the first moment he was able to distinguish his surroundings, for he followed every movement about him with his eyes.

It is impossible to describe the care which the mother took for everything which concerned the feeding and the safety of her newborn. She appeared always intelligent, and so cautious as to compel admiration. The slightest noise, the least movement aroused her to watchfulness and to anxiety for her young one, not for herself, for she was accustomed to men, and had become quite tame. All her movements were performed with the greatest dexterity, yet never so that the suckling could have come to any harm. The weight of her young one seemed in no way to hinder her movements, and no difference in her dexterity or activity was noticeable. But indeed it was apparent that she took great care not to strike her baby against anything. After about fourteen days he began to leave his mother and showed, even in his first steps, a dexterity and strength, the more astonishing since neither practice nor experience could account for it. The young Bunder, from quite the beginning of his active life, climbed the upright wire grating of his cage and scrambled up and down at will; he made also a few steps on the straw, sprang voluntarily from the height of his cage, alighting upon all four hands, then against the grating, up which he climbed with the ease and rapidity which had been noted in the adult. The mother followed every movement of her child with the greatest anxiety and seemed always ready to ward off any harm from her loved one. Later she sought, from time to time, to relieve herself of the burden, but remained always watchful, and at the slightest sign of danger snatched him up immediately. The slightest touch of her hand was also a signal to her ready pupil to return, and he would instantly take his accustomed position on his mother's breast. The leaping and play of the little animal became more perfect as his strength increased. I have often observed his merry gymnastics with the greatest delight and can attest that I have never seen him make a false movement, or fail to take measure of and reach the point for which he aimed. The little ape gave me certain evidence that he could estimate distance and control the requisite degree of strength for each of his leaps. From the first moment he knew his natural movements and how to accomplish by them what another animal, even though possessing the intelligence of a man, could have done only after countless trials and long continued practice. Here, indeed, one may ask: What can we say in explanation of the actions of animals?

After about six weeks a stronger nourishment than milk was necessary to the little ape, and here appeared a new phenomenon. Both animals showed a different aspect of their mental processes. The mother whom we saw before occupied with the most loving care for her offspring, who carried him constantly hanging to her body and breast, and of whom one would believe that, driven by maternal love,

[5] Brehm, A. E. Thierleben, 1887.

she was ready to give him the last bite from her own mouth, the same mother did not allow him to touch the slightest bit of food offered to him. As soon as the keeper had given them bread and fruit she took possession of it, thrust the young one away when he wished to eat, and hastily filled her cheek pouches and hands, so that there was nothing left for him. It would be a mistake to believe that a nobler motive than gluttony impelled her to this act. She could not have wished to force the young one to suck, for she had no more milk; no more could it have been care lest the food should be injurious to him, for he ate it greedily and thrived on it. Hunger now soon made him very bold, venturesome, and nimble. He could no longer be driven back by the mother's blows, and in spite of everything that she could do to keep her child at a distance and keep all for herself, the young one was always sly and quick enough to snatch one or another bit of food and to bolt it behind her back and as far from her as possible. This foresight was by no means unnecessary, for several times the mother ran to the furthest corner of the room in order to snatch back the food from her child. In order to ward off the results which must follow this unmotherly behavior we provided more supplies than the mother could eat or conceal in her mouth and in this way the baby was provided for. Thereafter he lived in good health and was fostered by his mother so long as he did not interfere with her food. He distinguished rather well people who fed or petted him. He was always goodnatured and, of the ape characters, showed only playfulness and agility."

That the rapid development of the Macacus monkey, so different from that of the human infant, is not persistent in the higher apes is shown in the following quotation from Wallace in which he compares a hare-lipped monkey (*M. cynomolgus*) with a young Mias or orang-outang which he had captured.[6]

"It was curious to observe the different actions of these two animals, which could not have differed much in age. The Mias, like a very young baby, lying on its back quite helpless, rolling lazily from side to side, stretching out all four hands into the air, wishing to grasp something, but hardly able to guide its fingers to any definite object; and when dissatisfied, opening wide its almost toothless mouth, and expressing its wants by a most infantine scream. The little monkey, on the other hand, in almost constant motion; running and jumping about whereever it pleased, examining objects around it, seizing hold of the smallest objects with the greatest precision, balancing itself on the edge of a box or running up a post, and helping itself to anything eatable that came in its way. There could hardly be a greater contrast, and the baby Mias looked more babylike by the comparison."

Finally, the following brief account by Ram Bramha Sányál is included as a description of these animals in their natural habitat.[7]

"The young monkey after birth attaches itself to its mother, and will not leave her for nearly a month, the mother nursing the young all the time with the utmost solicitude; after this time it will make little excursions on its own account, but is careful not to stray far, and at the slightest sound or movement it seeks refuge with her. The mother is unremitting in her vigilance over her offspring and in its personal wants and appearance. Compared with an orang-outang of the same

---

[6] Wallace, A. R. The Malay Archipelago, 1872.
[7] Ram Bramha Sanyal. A Handbook of the Management of Animals in Captivity in Lower Bengal, 1892.

age, a monkey is more helpful and intelligent, and in fact all its instincts are strongly developed at a comparatively early age. In about a month the young one begins to pick up grain and other food, and then the struggle for life soon begins, and the mother and the young one commence to fight over their food, although their natural instincts bind them to each other at other times."

SUMMARY OF DEVELOPMENT

Physical

At birth the little monkey was far advanced in physical development. His body, although less than 20 cm. in length, differed from the proportions of the adults to a much less extent than does that of most young animals. His head was disproportionately large, but not so much so as that of the human infant; his hind-quarters were considerably smaller proportionately than are those of the adult monkey. The body was covered with hair, distributed as in the adult with the exception of a peculiar bare line following the sagittal suture of the skull, where in the adult there is a heavy growth of hair. (This is shown distinctly in Plate II.)

The eyes were open at birth. They were at first light blue and did not reach the dark brown color of the adult until the ninth week.

As far as the crude methods employed could determine, the sensory development of the monkey seems to be complete at birth or shortly afterward; reactions to light appeared on the second day; painful and tactile stimuli brought responses on the first. The time of the beginning of the auditory function is not known with certainty but there is some evidence that sounds were heard on the second day. It was impossible to stimulate the other sense organs in order to determine their condition until much later, at which time they were completely functional.

The early, post-natal development was largely that of the motor apparatus, the range of activities keeping step with growth and increase in muscular strength. The rapidity of growth has been less than might have been expected to accompany the rapid increase in motor agility of the little monkey; the most marked increase in size being in the hind limbs. At the age of four months the baby has gained the proportions of the younger adults although his body length is less than one-half that of the adult.

The first teeth, the incisors, were cut during the fifth week; the molars did not appear until the 15th. Teething seemed to be somewhat difficult. The first manifestations of sexual activity were noted during the ninth week.

Sensory-Motor

First week. On the first day the little monkey was very still, moving only when forced to do so by the movements of the adult. However, certain reflexes seemed to be well established even on this day. Those observed were sucking, grasping, muzzling, crying, sneezing, winking (not in response to visual stimuli), inco-ordinated movements of the legs when the stimulus for grasping was removed, and an increased muscular tension of the legs in response to the mother's movements.

During the second day there appeared to be a slight unadaptive response to sound. In the human infant this varies in time of appearance from the second to the tenth day. By the third day his strength had increased so that his grasp upon his mother's hair had become secure. The head and eyes were at this age first turned to follow a moving object. Two days later appeared the reflex grasping at an object seen.

Second week. By the end of the first week his muscular activity was greatly increased, although most of his movements were still of the non-adaptive type. Complex co-ordinated movements of the limbs, as in jumping, appeared, and voluntary reaching toward moving objects became more frequent. The scratching reflex was established. On the 11th day he reached out and grasped small objects. By this time his responses to sound indicated some degree of localization. On the 12th day he first attempted to walk. The movements were very badly executed and showed a decided lack of co-ordination.

Third week. The third week, the first week of walking, was marked by a tremendous increase in his muscular control. The movements of the larger muscles of the limbs became fairly well adjusted to the demands made upon them, and many infantile movements were gradually made adaptive. The first definite play activities appeared, with contractions of the facial muscles in pursing the lips.

Fourth week. Play rapidly changed from simple pushing and grasping to the more complicated stalking and capturing of objects in the cage. This was closely connected with his increased interest in scraps of solid food, as he first attempted to eat at this time. The scratching reflex was perfected. The very complex behavior of the adult appeared suddenly complete. There is some evidence to show that he recognized food by sight within a few days after he first tasted it.

Fifth week. Apposition of the thumb and fingers was first observed, muscular co-ordination spreading peripherally. Crude experiments on his sensations of smell and taste indicated at least a discrimination of stimuli as indifferent and unpleasant. He attempted to draw the mother into his play.

Sixth week. The adult expression of anger or impatience, shaking his support violently, appeared suddenly. The thumb was used much more in grasping.

Seventh week. The first definite signs of interest in his own body were observed.

Eighth week. The use of the cheek pouches was acquired during this week.

Ninth week. Different vocal sounds were first distinguished. The method by which they were learned is not known, but from their sudden appearance they seem to have been instinctive rather than imitative. The first sexual activity was noted during this week.

By the 10th week the young monkey had become mature in all but the sexual activities. He was lacking chiefly in muscular control.

Fifteenth week. From the 10th to the 15th week the progress made was almost entirely motor. Play activities were still very marked and unadaptive movements persisted.

BEHAVIOR OF THE ADULTS

The maternal instinct in these animals seems to be limited to carrying and protecting the young one, permitting him to nurse and keeping him clean of parasites. Within these limits Dolly's care and watchfulness are unceasing, but beyond them she treats the baby much as she does the adults in the cage.

Her method of carrying and holding the baby is such as to afford him the greatest possible protection from enemies and from the weather. (Plates I and II.) Her patience in searching over his body for parasites is unlimited, greatly to the discomfort of the little one, to whose vigorous protests she pays no attention. No attempt at washing the baby, such as that described by Duvaucel [8] for the Gibbon, was ever observed. The rhesus monkeys are, in fact, quite careless of personal cleanliness.

The care of the baby brought about an interesting change in Dolly's relations to the other adult monkeys and to human observers. Where before she had been the most aggressive of the three, fighting for her food and keeping the others in fear of her, she now protected the baby by flight, showing a timidity quite at variance with her former disposition. The large male, Jim, was quick to notice this and soon became so savage in his attitude toward Dolly that it was necessary to put him in a separate cage.

The refusal of the mother to share her food with the young monkey has been noted with surprise by all observers of this species. Such a relation between parent and offspring is certainly rare among mammals and the extremes to which Dolly goes are without parallel. She has been observed to take food forcibly out of the baby's mouth and eat it herself, even when her own cheek pouches were distended to their full capacity. The significance of such an action is by no means clear. As Cuvier noted it is certainly not a means of protecting the young monkey from harmful food.

PLAY

We were particularly interested in the play activities of the young monkey from their bearing upon methods of experimentation with adults. On the whole, his play is very simple, consisting only of random infantile movements, climbing, and stalking. The first type appeared on the third day when he clawed at Dolly's face and arms.

The first complex play movement appeared in the third week. Beginning as a simple thrusting out of his hands against his mother it developed rapidly into the more complex stalking of various objects in the cage. At this time also he began to

[8] Duvaucel: cited by Huxley. Man's Place in Nature, 1909, p. 43.

take delight in climbing about the cage, twisting and turning in all directions and making little leaps to the ground. He sometimes appeared to wish to draw his mother into the play, stopping in the midst of his rapid climbing and striking out at her. For this, however, he was usually punished severely and so he never dared to persist in it. Often when Dolly lay down he would scramble back and forth across her body, but this is about the only familiarity she permitted him.

The stalking play was at first directed toward all conspicuous objects in the cage, but as the baby learned to eat solid food his attention became more and more directed toward this, and his play activities to center around it. In all his play there appeared many of the relaxed idiot type of movements, as well as purposive ones. Plate V shows this sudden undirected expenditure of muscular energy, which was at first induced by the sight of food or of any other interesting object.

"Self imitation," so marked during certain stages of development of the human infant, was almost entirely lacking. The few actions which might be so interpreted were those of climbing and leaping, in which certain movements were performed repeatedly, with evident enjoyment of the activity itself. It is just here that self imitation would be most valuable, since the activities requiring the most accurate judgment of organic stimuli are involved. In most of his play, however, his interest seemed to be centered in external objects rather than in the movements themselves.

LEARNING

Many of the little monkey's activities appeared suddenly, apparently without any preliminary practice, but others, particularly those requiring an adaptive response, were acquired only after many unsuccessful trials. New stimuli at first called forth an explosive reaction such as that shown in Plate V. Movements of all parts of the body were initiated, the reaction being wholly non-adaptive. Those random movements which resulted in manipulation of the stimulating object were repeated and the others gradually eliminated.

It is here that play seems to be of the greatest use, providing, as it does, a variety of undirected activities which are gradually moulded to meet the requirements of the environment.

DESCRIPTION OF PLATES

The photographs from which the plates were made were all taken during the fourth week.

PLATE I. The carrying position. The attitude of the monkeys in this photograph is not quite typical of the carrying position. Dolly has stopped and the baby is preparing to drop to the ground. He is consequently somewhat farther from Dolly's body than is usual.

PLATE 11.   The nursing and sleeping position.   Again this position is not typical
as the baby is turned partly away from Dolly.   One of his few imitative move-
ments is shown, the reaching out after his mother's moving hands.

Plate III.   His expression of fear is easily recognizable.   Immediately after this exposure was made he turned, chattering, to Dolly and was carried up to the shelf.

PLATE IV. The instinct to keep the baby free from parasites is very strong. Dolly forgets her dinner when a good opportunity to examine his back is offered.

PLATE V. The non-adaptive infantile movements, so frequent at this time, are illustrated here. Later such excessive movements were brought under control and made adaptive in play.

PLATE VI. The exposure was made after such a leap as that shown in Plate V.
The movement seemed to have been excited by the food but his leap did not
take him any nearer to it.

PLATE VII. The early lack of co-ordination in grasping is shown. Compare the position of his hands with that of the mother in Plates I and II. (The curious hump on the baby's back in this photograph is due to an error made in blotting out the background, which was not discovered until too late for correction.)

Fewer data are at hand with respect to the method by which the more complicated reactions were acquired, and indeed so little is known with certainty of the conditions of discrimination and learning in the adult that a discussion of the questions involved here does not seem advisable. There is, however, no evidence to show that the infant monkey ever gained a new activity by imitation. Walking, climbing, leaping, eating, and even the different vocal sounds appeared as instinctive acts which were merely perfected by practice. Dolly's movements sometimes served to draw the baby's attention to some object, but his own reactions to it never seemed to imitate hers. At times also, his responses appeared to be determined by those of the adults, as when Dolly's threatening attitude after some acts of the observer induced fright in him although he had not shown fear at the act itself. His response in such cases was, however, quite different from that of the adult and in no sense imitative.

In conclusion we may say that this paper is primarily a record of the facts of behavior observed in the development of the young monkey. So little is known with certainty of the more complex activities of the adults that any explanation of the actions of the infant monkey in terms of adult behavior is extremely difficult. In view of this fact it has seemed best to make little attempt to interpret the data at hand until the psychology of the adults is more thoroughly understood.

We wish to express our indebtedness to Mr. Donald Mackenzie, to whose patience in the face of the most unfavorable conditions the excellence of the included photographs is due.

OBSERVATIONS ON THE PREFERENTIAL USE OF THE RIGHT AND LEFT HANDS BY MONKEYS

SHEPHERD IVORY FRANZ

*From the Psychological Laboratory of the Government Hospital for the Insane,
Washington, D. C.*

In the course of a series of observations on the formation of simple habits by monkeys careful records were kept of the number of times each hand was used by an animal in taking the food which was presented. These observations are the data used in the preparation of the present communication. Six years previously I had observed that among a dozen monkeys certain ones tended to hold to the wire netting of the cage with one hand and to grasp with the other the food which was presented to them outside the cage. It appeared that there were marked individual differences, one animal apparently almost always using the right hand and arm for holding to the wire front of the cage and the left hand for taking the food, while another animal would reverse the hands in these two acts. These early observations were not systematically collected, but observations were made to determine whether or not it would be difficult to change the actions so that the animal which habitually used the right arm and hand to steady itself on the wire of the cage would learn to use that hand for grasping. It was found that after a few tests, twenty to thirty, in which the righthanded monkey was refused food when this hand grasped for it, and was given food in the left hand, this animal learned to hold with the right hand to the wire and to grasp for the food with the left. The ease with which the apparent habitual reaction was replaced by one of a different tendency led me to the belief that the apparent proneness to the exclusive, or almost exclusive, use of either hand might be due to any one of a number of extraneous factors, such as the position of the experimenter, his use of the right hand in delivering the food, etc. Further experiments to determine the truth or falsity of this belief were not made. Subsequently, the data presented in this paper were collected.

The monkeys used in this work were being trained previous to certain operative procedures on the occipital lobes.[1] They had been used in a previous investigation,[2] in which they had been fed from the front, sides, and bottom of the cage, and in which no attempt was made to have them use a special hand. During this latter investigation no observations were made of a preferential use of the hands. At the time the use of the hands was observed and the observations recorded, the animals were kept in cages 114 cm. high, 90 cm. wide, and 58 cm. deep. The front and right hand ends of the cages were covered with chicken wire, of one and one-half inch mesh. The top, bottom, the back and the left side were boarded. Within the cage there was a shelf 30 cm. wide jutting from the back of the cage at a height of about 45 cm. and extending the width of the cage. The animals were not handled and the environment, with the exception of the presence of the experimenter, was fairly constant during the progress of the experiments. Food and water, other than that used in the experiments were pushed through or under the wire front of the cage and the animal took of them when and as much as he wished. At the time of making the observations the animals were partly fed in the morning and the observations and tests made in the afternoon, or vice versa.

In performing the tests, the animal was in the cage, usually sitting upon the shelf. A glass plate, 12.5 by 18 cm., was arranged to hang horizontally on the wire netting of the cage, and was movable so that it could be placed upon any part of the front or right hand sides, i.e., those covered with the chicken wire. The food was placed upon the glass plate, this was arranged on the wire netting, and the experimenter moved away about a meter's distance. The animal, which usually during the preliminary arrangements sat at the farthest end of the cage, moved forwards and took the food. During the tests two pieces of food were presented, one of which was sweet, the other bitter. The arrangement of the relative positions of the two pieces of food was constantly changed so that half of the times the bitter bread was on the animal's right and half of the times on the left. At times the two pieces were

[1] For details see Franz. The Occipital Lobes. *Psychol. Review Monog.* No. 56, 1911.
[2] Shepherd. Some Mental Processes of the Rhesus Monkey. *Psychol. Review. Monog.* No. 52, 1910.

only about 3 cm. apart, and at other times they were as much
as 10 cm. apart. At all times they were sufficiently separated
so that both pieces were to be obtained only with difficulty
in one operation.

Observations of the number of times each hand was used
were made with six animals. Three of the monkeys were ob-
served from the beginning until the end of the experimental
series, and the other three were observed after they had formed
the habit of taking one piece (the sweet) and disregarding the
other (the bitter). Observations of two of the animals were
continued after the extirpation of parts of the occipital lobes.
The general results of the observations are given in tables I
and II.

TABLE I

Total Number of Times Each Monkey Used Right and Left Hands
During Period of Observation, Previous to Operation

Monkey	Right hand	Left hand	Totals
1	208	202	410
2	21	33	54
3	89	193	282
6	3	17	20
7	28	28	56
8	70	265	335
Totals	419	738	1157

TABLE II

Total Number of Times Each of Two Monkeys Used Right and Left
Hands During Period of Observation Following Operation

Monkey	Right hand	Left hand	Totals
1	108	21	129
8	30	0	30
Totals	138	21	159

Monkeys 1, 3 and 8 were the animals which were observed
throughout the period of training, and monkeys 2, 6 and 7
were observed only after the habit of taking the sweet food
was established. The results from the first set of animals are
the more interesting on account of the greater number of ob-
servations, although the results from the second set show the
same general tendency. Table I indicates that monkeys 1 and
7 were ambidextrous; monkeys 3, 6 and 8 showed a decided
preference for the left hand, and monkey 2 is in a doubtful

class since a slight change in the totals might throw him into either of the above classes. Table II shows that monkey 1 after the operation showed a decided preference for the right hand, and that in the few observations with monkey 8 a similar tendency was present. It is possible that the effects of the operation, although on the occipital lobe, may have had an influence on the animal's use of the hands, and for purposes of a general comparison these results may properly be omitted. These animals did, in fact, show inaccuracies in movement following the operation, but I was not able to determine any difference between the two sides of the body.[3]

In 114 of the tests with monkey 1, the animal took both pieces of bread, and in 182 tests only the sweet bread. When only the sweet bread was taken, the right hand was used 70 times, the left 112; when both pieces of bread were taken the right hand was used 52 times for both pieces (104 times), the left hand 28 times for both pieces (56 times), and in 34 tests both hands were used, one piece being taken in each hand. In all tests in which both pieces of bread were taken we may count that one piece was to the right and the other to the left of the animal; in the tests in which only one piece was taken the food taken was 93 times on the right and 89 times on the left. No account was taken of the positions of the pieces of food which were taken first when the two pieces were picked up, so that any correlation between the location of the food pieces is impossible for the total series. Only the occasions on which the animal picked up one piece can be used for this, and from the above figures (93 times on the right and 89 on the left) we find that the right hand was used for the picking up of the food 37 times on the right and 33 times on the left, and the left hand was used for taking the food which was 56 times on the right and 56 times on the left. In the case of this animal, therefore, the position of the food had no perceptible influence on the use of the individual hand.

In 185 of the tests with monkey 8, the animal took only one of the pieces of food which were before him; in 75 tests both pieces were taken. In the tests in which one piece of food was taken the right hand was used 32 times, the left 153 times; in the tests in which both pieces were taken the right hand was

---

[3] For details see my monograph, cited above, pp. 44-52; 95-97.

used 18 times for both pieces (total 36), the left hand 55 times (total 110), and both hands 2 (2 each). In the test in which the single pieces of food were taken the right hand was used for 15 pieces of food on the right and 17 on the left; the left hand 74 times for food on the right and 79 times for the food on the left. Although there is a slight difference in favor of taking the food on the left, the percentage is almost equal for both hands, and there is no apparent influence in this case of the position of food affecting the use of either hand.

The positions of the pieces of food in the tests with monkeys 2, 3, 6 and 7 were not noted on the records, and no data in regard to this matter can be given.

During the tests it was repeatedly noted that there were relatively long periods when each animal would use exclusively one hand in taking the pieces of food, followed by a period when the other hand was used. In a long series these alternations, if due to extraneous causes, should balance, but in the cases of monkeys 1, 6 and 8 after operation the series were not sufficiently long.

Although the data collected indicate as a whole that of six monkeys one showed an apparent preference for the use of the right hand (monkey 1), and two preference for the use of the left hand (monkeys 3 and 8), more observations are needed before any definite preferential use of the hands in monkeys may be accepted as proven. In view of the relation of the observations to the question of the origin of right or left handedness in man, the data are here given in the hope that other workers with monkeys may be tempted to make similar observations and publish their results.

NOTES

THE BEHAVIOR OF A GREY SQUIRREL

ELIOTT PARK FROST

Yale University

On last Thanksgiving morning the writer's lawn was covered by two inches of freshly fallen snow,—a depth sufficient to conceal all visible traces of the closely cropped grass. His attention was called to the behavior of a large grey squirrel, one of many that make their home in the neighborhood.

When first seen the squirrel was perched upon a wooden post some four feet from the ground, apparently making an interested survey of the landscape. From here he leaped lightly down across the snow, stopped abruptly and, raising himself on his haunches for an instant as if to detect possible disturbers, burrowed his nose in the snow and brought forth a buried nut. This he took in his mouth the length of the lawn, to the southerly, lee side of a large elm, where the snow was lightly fallen. Here the nut was superficially reburied under leaves, paws being chiefly employed.

Returning, the squirrel again climbed the post, surveyed the white ground as before, again skimmed across the lawn, and at a place 15 or 20 feet from the former cache, reclaimed another nut, transferred it to the elm, and similarly buried it with the first. The whole performance was repeated, while the writer watched, until eight nuts were brought together in one single cache. Three times he failed to climb the post before securing the nut. Once he burrowed without apparent result, but no further search was made. No two nuts were taken from the same place. Each nut found was unerringly detected and appropriated from under the untracked snow. At the conclusion of his task, which was performed in most business-like fashion in less than 10 minutes, the squirrel skipped away and was lost to view in a large elm across the street. This was the first snow-fall of the season. Whether the animal had weathered previous winters, the writer does not know.

Two distinct types of behavior are here correlated, first the precise detection and recovery of the buried nut; second, the assembling of the nuts at one single, protected spot. In his book, "Wild Traits in Tame Animals,"[1] Mr. Louis Robinson writes: "Squirrels will, without the least difficulty, find stores of nuts and acorns buried far from any tree or other perceptible landmark, even when the ground is covered by a recent layer of snow......" But the writer knows no literature which mentions the other type of behavior: the assembling and re-cacheing of food under these circumstances.

---

[1] Robinson, Louis. Wild Traits in Tame Animals. Edinburgh and London, 1897.

A REVIEW OF YERKES' AND WATSON'S "METHODS OF STUDYING VISION IN ANIMALS"[1]

By S. O. MAST

Nothing in the whole realm of literature on the behavior of animals shows as clearly as this monograph that we have outgrown the purely qualitative stage in this branch of science and have actually entered upon the quantitative phase. The monograph is indeed devoted almost entirely to methods designed for the prosecution and encouragement of work in this more advanced stage of the subject. The authors say on page 3: "Our standard procedures are recommended only for thoroughgoing, intensive, quantitative work. Simpler and more conveniently manipulated apparatus may be used in the case of preliminary exploratory work. We do not wish to discourage the use of crude and relatively uncontrollable methods for the study of vision, but we do most emphatically recommend that these methods be abandoned as soon as the rough problem-defining portion of an investigation has been completed."

These sentences state in admirable form the guiding principles of the whole investigation on methods. The authors apparently spared neither time nor labor in perfecting apparatus by means of which the ideal set forth in the quotation above could be attained. As a result we have an excellent description of the construction and working of a "Light or Brightness Apparatus" and a "Spectral Color Apparatus." Neither of these pieces of apparatus bears the slightest apparent relationship to the home-made variety with which most of us are familiar. They are in reality instruments of precision of the highest order, comparable in accuracy of construction and adjustment with a high grade microscope.

The light apparatus is adapted for the investigation of problems associated with brightness, size or form. By means of it animals can be simultaneously subjected to light from two sources, (1) of the same size and form but differing in intensity, (2) of the same intensity and size but differing in form, and

(3) of the same intensity and form but differing in size. The special relation of the two sources of light can be reversed and the intensity accurately controlled and measured.

The spectral color apparatus is designed for the investigation of problems concerning color. By means of it animals can be subjected, (1) to monochromatic light of various intensities and exceptional purity from any region of the spectrum, (2) simultaneously to two beams of light of precisely the same wavelength but of different intensities, and (3) simultaneously to two beams of light of different wave-lengths but either of precisely the same or of different intensities. The light in these beams can be selected from any two regions in the spectrum. Their relative position can be readily and almost instantaneously reversed. And the intensity can be accurately controlled, measured and compared in terms of energy.

It would be superfluous to attempt even a general description of either of these two pieces of apparatus. The monograph should be in the hands of every one in any way interested in reaction to light either in animals or in plants, perhaps not even so much owing to the discussion bearing on these special pieces of apparatus as to that bearing on the nature and experimental value of light artificially produced in various ways and that concerning the nature and production of colors by means of screens, filters and reflecting surfaces of various sorts.

ACQUIRED SPECIFIC REACTIONS TO COLOR (CHROMOTROPISM) IN *OREGONIA GRACILIS*

H. C. STEVENS

From the Psychological Laboratory of the University of Washington

Seven figures

I. INTRODUCTION

It has long been known that certain genera of the long-legged spider crabs place foreign bodies upon their legs and carapaces. This act is sometimes called a disguising and sometimes an act of decoration according to the interpretation which is put upon

it by the observer. In the citations which follow, disguise is the motive usually assigned to the animals. Thus in The Cambridge Natural History, "Crustacea and Arachnids"[1] Smith writes: "The Spider crabs do not burrow, and their respiratory mechanism is simple; but since they are forms that clamber about among weeds, etc., upon the sea bottom, they often show remarkable protective resemblances to their surroundings, which are not found in the cyclometopa. * * * But besides this, the long-legged forms such as Inachus, Hyas, etc., have the habit of planting out Zoophytes, Sponges and Algae upon their spiny carapaces, so that they literally become part and parcel of the organic surroundings among which they live. It may perhaps be wondered what are the enemies which these armoured crustacea fear." Similarly in the Riverside Natural History[2] the writer, J. S. Kingsley, states "Some of these forms keep their shells perfectly clean, seeming to rely upon their general resemblance to the Sertularians and other hydrozoa, among which they dwell, for protection. Others, however, permit all sorts of foreign bodies, both animal and plants, to become attached to their bodies, so that they are effectually concealed, and even when moving it seems as if a small forest of sea-weed were being transplanted to another locality." In the sentences just quoted the motive attributed to the animal is again concealment, although the foreign bodies are said to be permitted to become attached. Leunis[3] in discussing the same group of animals says of them: "Die meisten haben traege, langsame Bewegungen und tragen auf ihrer Oberfläche oft einen mehr oder weniger dichten Besatz von Pflanzen und festsitzenden Thieren (Hydroidenpolypen, Schwämen, u. s. w.) durch welchen sie leichterer vor den Nachstelligungen ihrer Feinde verbergen können."

It is evident from the quotations which have just been cited, that the authors entertain different views as to the manner in which the foreign bodies come to be upon the carapaces of the crabs. According to one, the Zoophytes, etc., are "planted out;" according to another, the plant and animal forms are "permitted" to become attached to the body of the crab. It soon

---

[1] Crustacea and Arachnids, p. 192.
[2] Vol. II, p. 61.
[3] Zoologie, Bd. II, 649.

became apparent to the writer, after a preliminary study of the habit of decoration in *Oregonia gracilis*, that a distinction should be made between what may be called *active* and *passive* decoration. Cursory observation of the crabs is sufficient to reveal the curious habit or instinct of self adornment. The animals do actually "plant out" algae, etc., upon their bodies. On the other hand, the writer doubts whether barnacles, tunicates, sponges, hydrozoa and tubeworms are placed upon the carapace by the active effort of the animal. Certainly, the writer never observed an active decoration of the crabs with such material, during a period of observation extending over seven weeks. Triton eggs were the only objects of a similar nature which were so used. On the other hand, the attachment of forms which simply happened to settle down upon the crab as it rested upon the bottom of the aquarium, was repeatedly observed. In one instance a sea-anemone (Metridium) 35 mm. in length when expanded, attached itself to the shell of a Mytilus which was already attached to the carapace of an *Oregonia gracilis* when captured. Passive decoration [4] must therefore be recognized.

The manner in which the active decoration or "planting out" takes place is worthy of description. Minkiewicz [5] supplementing his own observations by those of Aurivillius, has described the movements very exactly. "Le procédé de déguisement a été tres exactement décrit par Carl Aurivillius chez *Hyas araneus L.* de la famille des Majinae. Comme il est presque identique à celui de Maja, je n'y insisterai pas beaucoup. Ayant trouvé une algue (n'importe laquelle: rouge, brune, ou verte—cela dépend seulement de l'entourage), le crabe l'attrape avec ses pinces grêles et allongées, la met d'abord dans 'sa bouche' et en la tenant par un bout avec ses maxillipedes se met à la déchirer en morceaux avec les deux pinces, l'une l'attirant vers sa carapace, l'autre la repoussant.

[4] Since this paragraph was written, the author has found that C. Aurivillius made the same distinction and employed the same words as are here used, "Unter solchen Umständen stellt sich die *erste* und zwar die wichtigste Frage folgendermassen auf: Verhalt sich die Krabbe aktiv oder passiv hinsichtlich des Kleides fremder Organismen, welches ihren Körper bedeckt" P. 6, Die Maskirung der Oxyrhynchen Dekapoden durch besondere Anpassungen ihres Körperbaues vermittelt. *Svenska Vet. Akad. Handl.*, vol. XXIII. Stockholm.

[5] Analyse Expérimentale de l'instinct de Déguisement chez les Brachyures Oxyrhynques. (Note préliminaire.) *Arch. de Zoologie Expér. et Gén.*, t. 7, p. 36.

"Un morceau, de taille et de forme variable infiniment étant une fois découpé le crabe le pousse avec une de ses pinces entre les maxillipedes et le fait tourner plusieurs fois en procédant comme s'il s'agissait d'une proie, d'une moule ou d'un morceau de poisson par exemple.

"Apres l'avoir froissé, il le prend de nouveau avec une de ses pinces la gauche ou la droite sans distinction, puis étend la pince en avant autant que possible, et ayant fait un mouvement de rotation il recourbe la pince sur son dos, et se met alors à accrocher l'algue sur un groupe de crochets dorsaux, rostraux, branchiaux, etc., en maniant la pince a petits mouvements de va et viens, jusqu'à ce que l'algue se soit accrochée. Ou bien, il l'accroche sur la surface externe des pattes ambulatoires, également munies de crochets, en approchant la patte et en la pliant sous la face ventrale de la carapace.

"Les procédés sont identique, si l'on fournit aux crabes, à la place des algues, des éponges, des hydaires ou des ascidies composées S'ils ne trouvent pas des matériaux vivants ils se contentent de débris, de morceaux de carapace de crustacés morts, de coquilles, de tout ce qu'ils trouvent enfin: du papier, des chiffons, des fils, etc.''

The author has only to add that in the disguising or decorating of posterior portions of the carapace, the two posterior walking legs, in working upon the posterior portions of the carapace, play a part similar to that of the chelipeds except that, naturally, they are not able to prehend the object. The bit of alga, etc., is placed upon the extreme posterior portion of the carapace by the chelipeds. The right or left posterior walking leg extends, rotates medially and flexes in such a way as to bring the pointed terminal segment of the leg down upon the alga and by a sort of prodding movement affixes it to the carapace. In addition to the act of decoration, the crabs occupy themselves much with a kind of activity which suggests strongly the "preening" habits of birds. While thus engaged, the crab remains in the same place. The maxillipeds and the chelae are restlessly active. The chelae explore the dorsum of the carapace, grasp hairs and strip them lengthwise of whatever may be upon them. The result attained by these acts may be a cleansing.

The problems which are suggested by a study of the disguising reactions of the crab may be grouped as follows:

(1) By what means or instruments are the foreign bodies made to adhere to the body of the animal;

(2) By the action of what stimuli and by the execution of what responses is the disguising brought about;

(3) What end is sought, what purpose is served or what *telos* is realized by the series of reactions which results in a disguise.

The third of these questions may, from the author's point of view, be disposed of most easily. If the question means that the crab seeks some end of which it has any consciousness, or that the animal carries out a purpose of which it is dimly aware, the answer is that the crab seeks no end and carries out no purpose. Both end and purpose exist only for the anthropomorphizing human observer. From the point of view of such an observer, the crab does disguise itself, if to disguise means to alter the normal appearance of the body by the addition of objects which are foreign to it. The change of appearance in the body of the crab is the same to a human observer as would result if the animal were actuated by motives similar to those of a human individual consciously seeking to change his appearance with a wig and paint. Furthermore, the supposed "choice" of materials of the same color as that of the environment which Minkiewicz claims to have demonstrated, although all other observers have failed to confirm this result, may be explained upon the ground that in the natural habitat, the prevailing color of the environment is due to the most abundant material which, consequently, the crab meets with most frequently. Under the conditions which exist upon the littoral of the sea where the prevalent color tone is due to the most abundant material, the appearance of a harmony between disguise and environment results, which can not be confirmed under experimental conditions. Thus the purposiveness of this "harmony" turns out to be, like the purposiveness of the disguise itself, illusory.

In the experimental work about to be described, the effort was made to answer the first two questions.

II. EXPERIMENTS

The experiments were carried out during the summer of 1912 at the Puget Sound Marine Station, Friday Harbor, Washington.[6] Seven genera of the Majidae are found in the waters of Puget Sound: Hyas, Epialtus, Chorilia, Chionoecetes, Scyra, Pugettia and Oregonia. All seven forms (with the possible exception of Chionoecetes) show some tendency towards protective concealment, although the instinct is most marked in Oregonia gracilis which locally is known as the decorator crab.

[6] A systematic study of the plants and animals found upon Oregonia gracilis has been undertaken by Miss Evelyn Way under the supervision of Professor Trevor Kincaid, Director of the Puget Sound Marine Station. With their permission, the following incomplete list of plants and animals is here given to convey to the reader some idea of the variety of material found upon this crab.

PLANTS

Ulva
Polysiphonia pennata
Polysiphonia bipennata
Antithamnion
Antithamnion americanum
Kelp
Callithamnion
Ceratothamnion pikeanum laxum
Callophyllis flabellulata
Ectocarpus
Platythamnion heteromorphum
Pleonosporium vancouveranum
Nitophyllum latissimum
Dasyopsis plumosa
Bryopsis plumosa
Monostroma
Cladophora
Mesogloia andersoni
Desmarestia aculecata
Desmarestia ligulata
Dichtoniosiphon
Delessaria
Laminaria
Ceramium rubrum
Apoglossum
Fanchea gardneri
Iridea
Pterisiphonia dendroidea
Diatoms
  1. *Navicula grevillei*
  2. *Licmophora flabellata*

ANIMALS

Hydroids
  1. *Hydractinia aggregata*
  2. *Clytia edwardsi*
  3. *Perigonimus repens*
  4. *Tubularia harrimani*
  5. *Abelaria gelatinosa*
  6. *Abietinaria trashi*
  7. *Sertularella tricuspidata*
  8. *Plumnlaria setacea*
  9. *Selaginopsis mirabilis*
  10. *Thuiaria similis*
  11. *Abietinaria variabilis*
  12. *Aglaophenia struthionides*
  13. *Lafoea dumosa*
  14. *Lafoea gracillima*
  15. *Campanularia regia*
  16. *Sertularella polyzonias*

Sponges
  1. *Grantia sponge*
  2. *Volcano sponge*
  3. Six other varieties not identified

Anemones

Tubeworms

Barnacles

Little blue mollusc (*Mytilus edulus*)

Tunicates

Seamats

Mollusc eggs

Little white sea cucumbers

This species alone was used in our studies.   These studies were aimed at a solution of the following problems:

1. The color reactions of crabs which have been exposed to white light.
2. The color reactions of crabs which have been exposed to colored light.
3. The influence of the color of the environment upon the color of the material which is used for decoration.
4. The effect upon the disguising instinct, of blinding the crabs.
5. The orientation of blinded crabs to light.
6. The function of the dorsal hairs.

All reactions to color were carried out in a light-proof reaction box which was 45 cms. in length, 30.5 cms. in breadth, and 17.5 cms. in depth.   Two windows 8.5 cms. by 11 cms were cut in one end of the box.   A partition 10 cms. by 17.5 cms. was nailed to the bottom of the box midway between the two windows.   At the opposite end of the box, a V-shaped pen was made by nailing a strip of wood 10 cms. wide by 17 cms. long perpendicularly to the floor of the box and so placed as to bisect the corner angles of the box.   An opening 5 cms. in breadth was left at the apex of the pen and on the side towards the source of light.   Colored lights were obtained by placing colored glasses or filters in the windows which have already been mentioned.   See Figure 1 for a plan of the box.   A square hole, large enough to admit the head of the observer, was made in the lid.   Light was excluded by means of a hood of cloth.

The sources of light were three glasses and two filters.   The glasses were ruby red, a green, and a colorless glass.   The color analyses and spectral transmission of these glasses were made by the Bureau of Standards of the United States Government. These analyses are given below.   According to a statement made by the Director of the Bureau of Standards, "The properties of the clear glass are so nearly those of absolutely colorless glass that we have not undertaken the very expensive investigation that would be necessary to determine them." The yellow light was obtained by means of a potassium dichromate solution (10 gms. to 300 cc. of distilled water) contained in a flat-sided glass filter the cubic dimensions of which were

approximately 10 x 16 x 3 cms. The glass walls of the filter
were 5 mm. in thickness. Blue light was secured by an am-
moniacal solution of copper sulphate (10 gms. of copper sul-
phate to 300 cc. of water plus 10 cc. of ammonia). This solu-
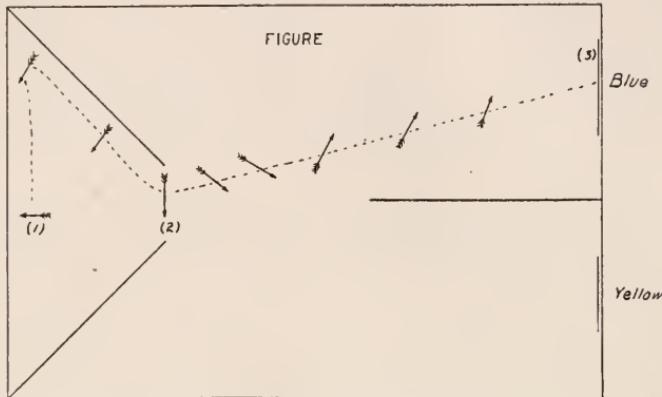
Figure 1 shows the reaction of Specimen 12 (VIII-25-1912, 12.30 P. M.) to blue
   and yellow light. The head of the arrow indicates the head of the crab. The
   dotted line indicates the path. The time spent in moving from (1) to (2)
   was 25 seconds; from (2) to (3) 10 seconds.
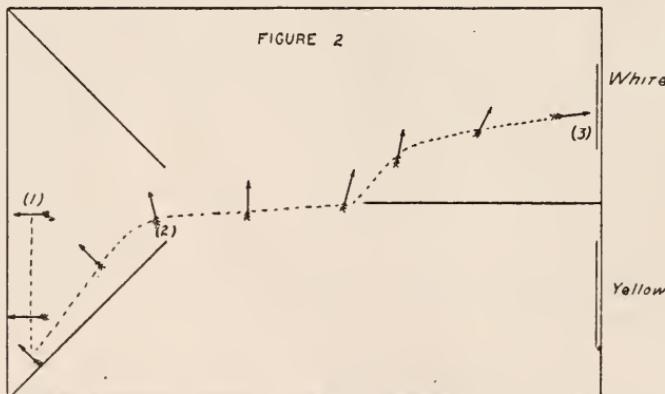
FIGURE 2 represents the reactions of the same crab as shown in Figure 1. The
   time spent in moving from (1) to (2) was 30 seconds; from (2) to (3) 20
   seconds.

tion was placed in a filter similar in form to that which con-
tained the solution of potassium dichromate. The tops of both
filters were covered with a glass plate and sealed with balsam.

   The color analyses and the spectral transmission of the lights
as determined by the Bureau of Standards are here given:

Color Analysis

	Dominant Hue	Per Cent White	Total White Transm.
Green glass............	540	47	39.6%
Red glass.............	650	26	1.3
Yellow liquid (1 cm.)....	584	18	51.2
Blue liquid (1 cm.)......	468	45	14.1

Spectral Transmission

Wave Length	Red Glass	Yellow Liquid 10 mm.	Green Glass	Blue Liquid 10 mm.
430 $\mu\mu$	0.0	0.0	5.2	69.9
40	0.0	0.0	7.9	64.8
60	0.0	0.0	24.2	52.2
80	0.0	0.0	41.8	30.6
500	0.0	0.0	59.8	30.6
20	0.0	0.0	68.0	16.0
40	0.0	36.0	62.9	7.6
60	0.0	80.8	48.3	3.4
80	0.5	90.5	35.6	1.8
600	1.4	95.0	27.1	1.2
20	6.4	96.8	18.0	1.2
40	16.4	97.3	12.7	1.2
60	26.5	97.1	10.4	1.7
80	34.6	97.0	8.5	2.2
700	42.1	97.1	7.9	3.4
20	44.7	97.1	7.0	4.9
40	45.0	97.1	7.4	6.6

The reaction box was attached to the wall of an aquarium which floated in the Sound. This aquarium was about 160 cms. in length by 120 cms. in breadth by 60 cms. in depth. The long dimension of the aquarium was approximately northeast by southwest. The reaction box was attached by its long side to the southeast wall of the aquarium with its two windows facing the northeast. The box was submerged to a depth of 12.5 cms. Inasmuch as the experiments were made for the most part in the morning at approximately the same time (from 9 a. m. to 11 a. m.) a certain constancy of illumination was secured. The specimens were collected from time to time as they were needed. When not being used for reactions they were placed in the aquarium above described. This aquarium proved to be very suitable for marine plant and animal life as very delicate deep-sea forms throve in it for weeks at a time. The attempt was made to secure reactions to light from the crabs when the box was out of the water. These attempts proved unsuccessful. The reaction box was therefore submerged to the depth already mentioned which was sufficient to cover the windows. In this way, the intensity of the light was cut

down by a constant but unknown amount. When the head of the observer was introduced into the opening in the lid of the box and all light excluded by means of the hood, the only sources of light were the two windows which appeared brightly illuminated. Even with the least bright colors, red and blue, with dark adaptation of the eyes of the observer, the movements of the crab could be seen.

In the study of the reactions to light, the mode of orientation of the animal and its final position with reference to the source of light were observed and two times were measured. The two times were those which elapsed from the moment when the crab was placed in the V-shaped pen until the moment it emerged from the pen; the other time was that which elapsed from the moment of emergence from the pen until the source of light was reached. See Fig. 2. Inasmuch as the crab is an exceedingly thigmotropic individual, the length of time which passed in the pen before emergence was very variable. On the other hand, the time between emergence from the pen and the reaching the source of light, which I shall speak of as the reaction time to light, was much more constant, although subject to considerable variation both with respect to the lights and to the animals used. The times of emergence from the pen and the attainment of the light were signalized by the observer whose head was in the reaction box by snapping the fingers. An assistant outside who held a watch recorded the time. The movements of the crabs are very deliberate so that the second is a sufficiently small unit in which to measure the reaction time. In the study of the orientation of the animal each change of position, from the position in which it was placed in the pen, until it reached the source of light, was recorded by the observer upon a diagram of the interior of the reaction box. A record was thus kept of each crab's route as it passed from the pen to the windows.

Under the conditions of the experiments two variable factors entered into the behavior of the crabs in such a way as to modify their reaction times and their modes of orientation. These factors were thigmotropism or its more special form of "goniotropism," as Minkiewicz calls it, and habituation. At the beginning of a reaction experiment, the crab was placed in the middle of the V-shaped pen with its cephalothorax away from the source

of light and the mid-line of its body coinciding with the middle
line of the reaction box. With only one or two exceptions, the
first movement of the animal was towards the rear wall of the
pen, then to right or left to the corner of the box. On reaching
the corner, the animal usually turned to right, if it occupied
the right corner, (the observer is supposed to be facing the
windows) or to the left, if it occupied the left corner in such a
way that long axis of its body was perpendicular to the oblique
partitions of the pen and the walking legs on one side of its
body in contact with the rear wall of the box. On moving out
of the pen, progress was always a sort of sidewise sidle along
the oblique partition of the pen, with the long axis of the body
perpendicular to the wall and the walking legs of the side exposed
to the light reaching out along the floor and wall. On emerging
from the pen, the long axis of the animal's body was transverse
to the long axis of the box, but exactly on the middle line of
the box. One side of the crab was, therefore, exposed to the
action of the light from the two windows. Since the oblique
wall of the pen made an angle of about 45 degrees with the
side of the reaction box, it is evident that the long axis of the
crab must have rotated through an angle of 45 degrees before
it could become transverse to the long axis of the box. Such
a rotation did actually take place when the crab arrived at the
end of the oblique partition. The posterior walking legs on the
side towards the light would reach around the end of the par-
tition and swing the body of the crab into a position at right
angles to the long dimension of the box. In very rare cases
when the crab was very weakly positively phototropic, the
movement of rotation would continue until the animal was
completely outside the pen but still in contact with the parti-
tion, the long axis of its body perpendicular to the partition,
as ever. In these rare cases, the animal would sometimes con-
tinue its side-wise progress until it occupied the corner at the
rear of the box between the oblique partition and the side. In
the typical reaction of a majority of positively phototropic
crabs, the animal, on emerging from the pen, struck out without
hesitation along the middle line of the box until it reached the
medial partition between the two windows. Upon contact with
the partition, rotation would occur, sometimes with a slight
hesitation, usually, however, without, and the animal would

continue into the open space, exclusively lighted by one of the windows. It is to be noted that up to the time that the middle partition is met with, locomotion is in a side-wise direction, with reference to the long axis of the crab's body. On orienting to the light, after coming in contact with the partition, rotation occurs about the posterior mid-point of the carapace, in such a way that the anterior end of the animal is directed towards the light. As the crab moves towards the light, with the long axis of its body obliquely disposed with reference to the length of the box, as a result of the rotation just described, further rotation of the long axis of its body with reference to the long axis of the box takes place, with the result that the anterior end of the body is turned directly towards the source of light and both sides of the body are equally illuminated. This type of orientation is shown in Fig. 2. This rotation of the body so that the light fell equally upon both sides, was very striking with the white and green glasses. With red it was least. Blue probably stands next to red in this respect, with yellow next to green. In a considerable proportion of the reactions, the crabs, upon emerging from the pen, rotated towards the light (from the transverse position with reference to the mid-line of the reaction box, which they always occupied on leaving the pen, to the right or left according as the head was pointed to the left or right), immediately, without advancing to the partition in the manner which has just been described, and struck out in an oblique direction towards the right or left source of light. This type or orientation is shown in Fig. 1. As the animal advanced towards the light, the anterior end turned more and more as the window was approached, until, when it arrived, both sides were equally exposed to the light. An analysis of the reactions has been made with view to finding out what proportion of the reactions ended in the manner just described and what sort of glass caused such reactions. Out of a total of 105 reactions in which the head was directed towards the source of light with each side of the body equally exposed to it, 47 were reactions to white, 24 to green, 17 to yellow, 14 to blue and 3 to red, light. Without entering into a discussion of theories at this point, it may be pointed out that these results seem to show that unequal intensity of stimulation of the two sides of the crab's body is the chief factor in orientation.

In describing the manner in which the crabs behave after being released in the pen with the anterior end facing towards the rear of the box, it was stated that some of the animals moved to the left and some moved to the right corner of the pen. It was shown, furthermore, that the animal sidled along the oblique partition of the pen and finally emerged with the longitudinal axis of its body transverse to the mid-line of the box and with its cephalothorax pointing either to the right or left, so that the right or left half of the body only was exclusively stimulated. The question naturally arises whether the side of the body (right or left) which is exposed to the light influence to any extent the window (right or left) to which the animal reacts. An analysis of the reactions with respect to this point shows that out of 198 reactions, the crab emerged from the pen with the head towards the right side of the box, 63 times. Of these 63 reactions, 31 reactions were to the light in the *right* window, and 32 reactions to the light in the *left* window. The distribution is exactly what one would expect if chance alone were operative. In 135 cases the crab emerged from the pen with the head directed to the left side of the box. Of the 135 cases, 72 went to the *left* light and 63 to the *right* light. Although the figures show an excess of 9 in favor of the left window, the author considers this only such a deviation from the distribution according to chance as is to be expected from a small number of reactions. On the other hand, the head upon emergence from the pen was turned to the right in 63, and to the left in 135, cases. This difference is too great to be attributed to chance. Some influence must have been at work to determine the predominance of the reactions with the head towards the left. This influence might conceivably be resident in the reaction box itself, in the crab or in some circumstance outside of the box. As far as could be seen, the right and left sides of the box were exactly alike. So far as is known the two sides of the body of the crab are identical. Of the circumstances existing outside of the box, there is the fact that the observer sat upon the right side of the reaction box. It seems likely, therefore, that the observer in some unknown manner, either in placing the crab in the pen or by the mere presence of his body upon the right side of the box, influenced the initial turning of the crab.

The other general factor, besides thigmotropism, which influenced orientation was habituation to the reaction box. Inasmuch as five different stimuli were used, it is evident that each compared with every other gives 10 combinations. Since each stimulus was presented first upon the one side and then upon the other, the total number of reactions for the five lights was twenty for each crab. The usual order of the reactions is shown in Table I. With an animal which reacted tolerably briskly, a series could be completed in one hour. With most crabs, however, the time was much longer for the reason that the animal seemed to become habituated to the conditions existing in the box. The first few reactions were usually rapid. As the series lengthened, however, the duration of the time spent in the pen increased, until in many instances the work had to be abandoned for that particular day.

TABLE I

Shows the Order in which the Colored Lights were Exposed in the Reaction Box, the Numbers Indicate the Number of the Experiment in the Series. The Right or Left Position of the Figure in the Column Indicates the Right or Left Position of the Color at the Top of the Column. Thus Experiment 6 in the Table Means that Red was Presented on the Right side of the Reaction Box with Blue on the Left.

	R		Y		G		B	
Y	1	2						
G	3	4	9	10				
B	5	6	11	12	15	16		
W	7	8	13	14	17	18	19	20

1. *The color reactions of crabs which have been exposed to white light.*—Ten specimens of Oregonia gracilis were used, the sex and number of which are given in the following table. The five lights, with the general arrangements already described, were presented in pairs with an exposure of each color upon the right and left sides. A complete series consisted, for each individual, of 20 reactions, arranged as shown in Table I. This number was secured for every crab except Specimen 9 whose series consists of 18. Although this animal was exposed to the action of the blue and white lights on four successive days,

(September 2, 3, 4 and 5) no reaction was obtained. Counting each reaction for each animal as an observation, the total number of observations under these conditions was 198. The distribution of the reactions with respect to each light and to each crab is given in Table II. The letters L and R indicates whether the light occupied the left or right window of the reaction box.

TABLE II

Specimen	Red		Yellow		Green		Blue		White		Total
	L	R	L	R	L	R	L	R	L	R	
3 ♀	0	1	1	1	4	3	2	2	3	3	20
4 ♀♀	1	0	3	2	2	2	0	2	4	4	20
7 ♀♀	0	0	1	2	2	2	3	2	4	4	20
8 ♀	0	0	1	3	3	2	2	1	4	4	20
9 ♂	0	0	2	2	3	2	2	2	2	3	18
12 ♀♀♀	0	0	2	2	2	1	2	3	4	4	20
13 ♀♀	2	0	0	2	3	2	1	2	4	4	20
14 ♀	2	1	1	1.	2	2	2	2	3	4	20
15 ♀	0	1	2	2	3	2	1	2	4	3	20
16 ♀	2	3	3	0	1	1	0	2	4	4	20
	7	6	16	17	25	19	15	20	36	37	
Total	13		33		44		35		73		198

It will be seen from the table that the white light received most of the reactions, with green next, then blue and yellow about equal, and finally red least of all. The table also shows in which window (right or left) the light was exposed when it was reacted to positively. It will be seen that with red, yellow, and white the reactions were divided about equally between the right and left windows. With green there is an excess of 6 in favor of the left window; while with blue there is an excess of 5 in favor of the right window. The author considers these deviations from the distribution according to chance, to be non-significant, although he is unable to account for them. Figure 3 shows by means of a graph the distribution of the reactions with respect to lights, which are exhibited in Table II.

The reaction times of the ten crabs which were used in this set of observations have been determined and grouped. The time measured was the time in seconds which elapsed between the emergence of the animal from the V-shaped pen and the

attainment of the window. The individual reaction times for each light and for each specimen are shown in Table III. The numbers mean number of seconds.

2. *The color reactions of crabs which have been exposed to colored lights.*—The object of these experiments was to determine whether Oregonia gracilis possesses a chromo-kinetic resonance in the sense in which that term is used by Minkiewicz. The experiment upon which Minkiewicz bases his conclusion that a chromo-kinetic resonance exists is described by him in the following passages. "On met les crabes dans les aquariums préparatoires, chacun d'une couleur différente et ne contenant que du matériel de déguisement de la même coleur. On divise
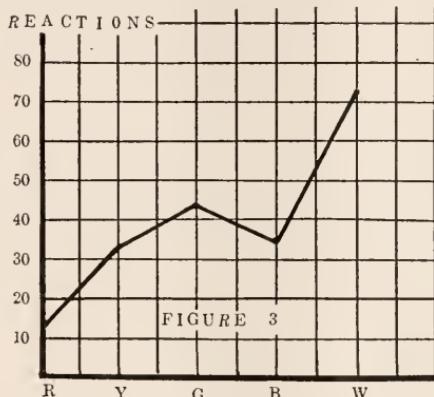
FIGURE 3 represents the distribution of the reactions with respect to lights.

un autre aquarium en deux moitiés diversement colorées et on y transporte les crabes une fois revêtus dans les aquariums préparatoires.

"On voit alors, les crabes se diriger constamment vers la moitié de l'aquarium dont la couleur correspond à celle du papier de leur revêtement et y rester pendant longtemps. Ainsi, par example, dans l'aquarium rouge-vert les crabes rouges se dirigent vers le milieu rouge, les crabes verts vers le milieu vert.

"L'expérience la plus frappante était celle faite dans l'aquarium divisé en trois partie égales, dont la médiane était colorée en blanc, les deux autres en noir. Les crabes blancs gagnèrent la partie médiane (blanche) et restèrent là pendant toute la durée de l'expérience (quelques heures). L'expérience de con-

TABLE III

Shows the Duration and Distribution of the Reaction Times for Each Specimen and for Each Light

Specimen	R	Y	G		B	White	
3	70	15 19	50 10 36 150	145 55 80	33 15 27 24	37 60 20	60 27 16
4	30	10 10 10 40 55	17 25 35 7		10 15	10 20 10 8	11 5 8 10
7	0	20 90 25	30 30 20 25		16 10 10 30 15	15 20 25 15	15 22 15 15
8	0	25 40 10 10	35 7 12 10	5	5 10 60	9 15 5 · 35	20 5 15 10
9	0	15 40 5 65	45 75 90 8	240	40 135 15 300	255 5 20 5	65
12	0	15 40 10 5	25 20 15		10 30 10 25 10	10 20 10 20	20 25 15 20
13	10 · 147	3½ 4	7 3 7 10 4		40 18 5	7 7 10 50	11 13 10 8
14	16 12 42	14 8	55 7 12 10		23 80 8 10	9 9 8 12	7 8 9
15	15	15 12 20 34	22 40 27 15	9	15 34 17	21 25 28 21	12 50 15
16	13 56 188 15 13	8 13 240	13 35		23 33	10 · 10 31 24	34 53 62 36

trole dans l'aquarium blanc-noir-blanc me donna le même résultat pour les crabes noirs."[7] The "choice" of costume is thus explained.[8] "L'animal mis dans un milieu coloré—vert, par example—en acquérant sous l'influence directe du milieu, par résonnance chromo-cinétique, le chromotropisme correspondant (synchrome), devient *chlorotrope* et par conséquent négatif vis-a-vis des autres couleurs. S'il trouve des papiers de couleur, il ne peut prendre, c'est-a-dire s'approcher, ni des rouges ni des blancs, etc., ces couleurs faisant dans l'aquarium vert des surfaces négatives (repoussantes) pour l'animal accordé chlorotropiquement. Or, il se déguisera en vert, qu'll rencontrera en errant sur les surfaces verts. * * * Il en est de même dans un milieu de n'importe quelle couleur excepté le milieu de noir." Minkiewicz here contradicts a statement which is made in the first of the two citations where he says "L'expérience de controle dans l'aquarium blanc-noir-blanc me donna le même resultat pour les crabes noirs." Briefly put, Minkiewicz's doctrine states that the light receptor system of the crabs, together with their central connections, acquire, by exposure to light of a certain wave length, a specific sympathetic, resonance (synchrone resonnance). By virtue of this specific, sympathetic, resonance, ambulatory movements are initiated which are specific, in the sense that they carry the animal fatally towards the source of light of the same wave length as that to which it has been exposed. Hence the chromo-kinetic-resonance. To obtain experimental evidence upon this subject, a series of observations was made in which certain crabs were exposed to different colored lights for a period of time from 24 to 36 hours in length. It was assumed that such a period was sufficient for the animals to acquire the chromo-kinetic resonance, if such exists. After exposure to the action of the lights, for the times stated, the crabs were placed in the reaction box and their reactions to a series of lights, presented two at a time, one of which was the light to which the animal had been exposed, were determined. The lights used in the reaction box were those used in the experiments already mentioned. The colored light to which the crab had been exposed was presented with each of the other four lights, first on the right, and then on the

[7] Analyse Experimentale, p. 41.
[8] Ibid., p. 54.

left, side.   Eight reactions were thus obtained, in which the animal was given the opportunity to react either to the color to which it had been exposed or to another.   Although one color was thus exposed 4 times to once of each of the other colors, it is the author's opinion that the results are not vitiated by this procedure.   Evidence for this position is furnished by the reactions of Specimen 16, from which a complete series of 20 observations was obtained.   Although this individual was exposed to the action of red light for 24 hours prior to the reactions, a marked chromo-kinetic-resonance is apparent which is not altered in any way by the subsequent reactions to the other lights.   It seems reasonably certain therefore that had a full series of twenty reactions been obtained from each of the other specimens which had been exposed to a certain light, the results would not have been different from those actually obtained.   Furthermore, as appears from Table I, which shows the order in which the lights were presented, in the experiments recorded in Table II red was shown 8 times, yellow 6 times, green 4 times and blue 2 times in succession.   Yet in spite of the inequality in the order of presentation, there is no evidence whatsoever that the light which was exposed most often in succession, received most reactions.   In fact red which heads the list in this respect, was reacted to least frequently.   The results which follow, therefore, can not be explained upon the assumption of an undue influence of the color from the frequency of its successive presentation.

The aquaria in which the crabs used in this series were exposed to colored light for 24 hours prior to testing their reactions in the manner just described, were made by painting the insides and bottoms of galvanized iron pails.   The diameter of the top was 250 mm. that of the bottom 212 mm.   The depth of the pails was 250 mm.   The area of the sides and bottom is equal to 2063.85 sq. cms.   The color of the paints can not be characterized very definitely.   The red was a vermilion; the blue an ultramarine;   the green a "dark" green;   the yellow a "lemon" yellow.   The aquaria were suspended in the large aquarium already described, in such a manner that their tops were about 3 cms. under the surface of the water.   In this way, a supply of fresh water was secured.   The observations in the reaction box were made immediately after taking the animals

from the colored aquaria. The procedure of these experiments
was exactly the same as that already described. The general
type of orientation, the effects of thigmotropism and habitua-
tion, the length of the reaction times were about the same as
those described above. The results of these experiments are
shown in Tables IV, V, VI and VII; and their corresponding
Figures, 4, 5, 6 and 7. Each centimeter of the cross-section
paper indicates one reaction.

TABLE IV

Shows the Reactions of Individuals which Had Been Exposed to
Red Light

Specimen	R	Y	G	B	W	Total
21 ♀	1	2	2	1	not used	6
16 ♀	5	1	0	0	2	8
	6	3	2	1	2	14
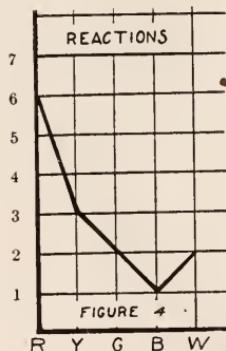
FIGURE 4. Shows the curve of distribution of the reactions of Table IV

It appears to be very certain, judging from the results of
these experiments, at least, that the color reactions of *Oregonia
gracilis* are influenced in a dominant degree by the color of the
light to which the crab is exposed. The curves show clearly
that the maximum number of reactions invariably falls to the
colored light of the same quality as that to which the animal
has been previously exposed. Of the ten specimens used in
this series only two, Specimens 18 and 21 failed to react maxi-
mally to the light to which they had previously been exposed.

With the other eight crabs, the majority of the reactions fall to the colored light used in the preparatory stimulation. There exists, therefore, very strong, although not absolutely conclusive, evidence that *Oregonia gracilis* acquires by exposure to the action of colored lights, a specific chromotropism for the light thus used.

TABLE V

SHOWS THE REACTIONS OF INDIVIDUALS WHICH HAD BEEN EXPOSED TO YELLOW LIGHT

Specimen	R	Y	G	B	W	Total
22 ♀	0	3	2	1	2	8
23 ♀	1	3	2	0	2	8
.	1	6	4	1	4	16
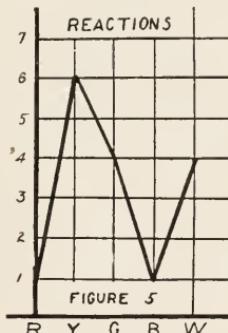
FIGURE 5.   Shows the curve of distribution of the reactions of Table V

TABLE VI

SHOWS THE REACTIONS OF INDIVIDUALS WHICH HAD BEEN EXPOSED TO GREEN LIGHT

Specimen	R	Y	G	B	W	Total
17 ♀	1	1	3	1	2	8
18 ♀	2	1	1	2	2	8
19 ♂	1	1	4	1	1	8
20 ♀	1	1	2	not used	not used	4
	5	4	10	4	5	28

3. *The influence of the color of the environment upon the color of the material used in decoration.*—The experiments of this section were devised to determine whether the color of the material used by the crab in decoration bore any direct relation to the color of the environment. The same four colored aquaria as were used in the experiments upon the chromokinetic resonance were employed here. The colors were red, yellow, green and blue. A black aquarium was added, as it was stated by Minkiewicz that the animals do not decorate themselves in black aquaria. The general plan of the experi-
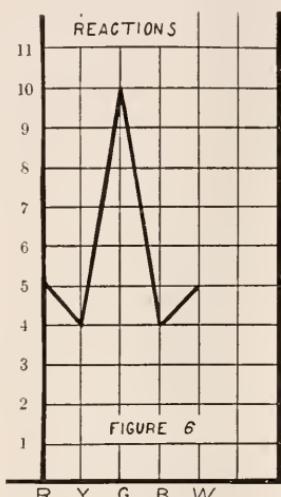
FIGURE 6. Shows the curve of distribution of the reactions of Table VI

ments consisted in carefully stripping off all detachable decorations from five individuals and placing each of them in one of the colored aquaria. Colored tissue papers of the same dimensions were also placed in the aquaria. The animals were left in the aquaria for a period of several hours, usually over night. Three series of experiments, in which five different crabs were used in each series, furnish the evidence upon which our conclusions are based.

First Series

IX–3–1912. 12:30 P. M. Five individuals were carefully cleansed of all algae, hydroids, etc. Ten pieces, 5 x 5 mm., of each of five colored papers were placed in the aquaria. The

colors of the papers were red, yellow, green, blue and black. These papers were not standardized with reference to any code. Results: At the end of 36 hours, no individual had used any piece of paper for decoration. During the time that the crabs were under observation, they moved about the bottom of the aquarium, trying vainly to escape. At times they remained

TABLE VII

Shows the Reactions of Individuals which Had Been Exposed to Blue Light

Specimen	R	Y	G	B	W	Total
24 ♂	0	0	2	4	2	8
25 ♀	1	0	1	4	2	8
	1	0	3	8	4	16
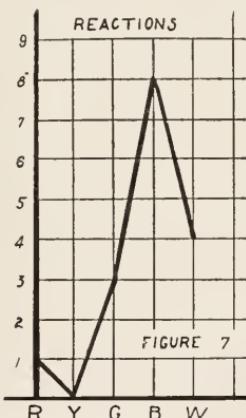
Figure 7. Shows the curve of distribution of the reactions of Table VII

motionless and busied themselves with "preening" their hairs. They seemed not to notice the presence of the paper.

Second Series

IX–9–1912. 5 P. M. Five crabs, two males and three females, were carefully cleansed of all decoration and placed in the aquaria. Five pieces, 10 x 10 mm., of each of five colored papers were placed in the aquaria. A piece of dead clam was also added. The animals ate voraciously and "preened" themselves.

Results: IX–10–1912. 3:30 P. M. Red aquarium. Male. Crab was alive. Not decorated, although ulva had floated in. Yellow aquarium. Female. Animal alive. Decorated with green ulva which floated in during the night. Green aquarium. Female. Animal alive. No decoration, although ulva had floated in. This was 10.30 A. M: Cleaned out aquarium and placed in it two new individuals carefully cleansed. At 3:30 P. M. same day, there was no decoration. Blue aquarium. Male. Crab alive. Not decorated. Black aquarium. Female. Animal alive and gaily decorated with torn pieces of the colored paper. There were six pieces of green, four of blue and two of yellow. No crab ever made use of the papers to the extent of this individual. Killed IX–11,1912 and preserved in formalin.

Third Series

IX–11–1912. 5:30 P. M. The five aquaria and five crabs carefully cleaned. Five strips, 10 x 60 mm., of each of the five papers were placed in the aquaria. Results: 9 A. M. IX–12–1912. Red aquarium. Female. Animal alive. Not decorated. Yellow aquarium. Female. Animal alive. Not decorated. Green aquarium. Male. No decoration. Animal alive. Blue aquarium. Female. Animal escaped. Black aquarium. Animal alive. Decorated with a large piece of red paper on its rostrum and an entire strip of blue paper on its carapace. Preserved [9] in formalin IX–12–1912. 10 A. M.

The chief conclusion to be drawn from these experiments is that these crabs do not decorate themselves with materials of the same color as the color of their environment. Our experiments therefore support the results of Pearse, Mast and others who have carried out similar experiments upon *Libinia emarginata*. One is surprised at the prevalence of the view that these animals "choose" colors of the same color as their environment, when the evidence upon which this view depends for its support is critically examined. Minkiewicz is the only experimenter who has given assent to the doctrine of selective, protective, concealment. And while he attempts to explain the reactions which result in concealment in a purely mechanical

---

[9] Formalin was unfortunately chosen as the preserving fluid. It was hoped that individuals might be preserved for demonstration purposes with all their regalia on them. The action of the formalin, doubtless as a result of the aldehyde, has almost completely bleached the colored papers.

manner, which as a general mode of explanation of animal behavior is entirely acceptable to the writer, the experimental work upon which Minkiewicz bases his conclusions has never, to the knowledge of the present writer, been satisfactorily presented in any scientific journal. Without exception, Minkiewicz's experiments have been stated in a general form so involved in theoretical considerations that the facts themselves ascertained by experiment have never received proper attention. Until Minkiewicz publishes the actual results of his experiments and not the inferences which he wishes to draw from them, his scientific colleagues will be justified in accepting the alleged results with reservation.

A second conclusion which can be drawn from our results is that the size of the paper placed in the aquarium has a distinct effect upon the use of the paper for decoration. With bits of paper 5 x 5 mm. no decoration at all occurred. With the larger pieces decoration resulted in both cases. In view of the results obtained from the blinded crabs it seems likely that the stimulus to the decorating instinct is tactile. Those pieces of paper sufficiently large to catch upon the chelae of the crab excite the decorating response. Those pieces, like our 5 x 5 mm. pieces, which are so small and tenuous as to give no adequate stimulus to the claws of the crab, are passed over unnoticed.

4. *The effect of blinding upon the decorating instinct.*—Early in the experiments, the attempt was made to determine by means of an *experimentum crucis*, the rôle played by the eyes in the decorating reactions. On the assumption that the reactions were responses to visual stimuli, for on no other assumption could the supposed harmony between the color of the decoration and the color of the environment be explained, the elimination of the eyes would abolish the response, unless some other stimulus than visual, could set off the instinct. If some other than a visual stimulus could initiate the response, the resulting decoration ought to bear no relation to the color of the environment, unless the crab possesses color-sensing organs other than the eyes. The result of the next section on the reactions of blinded crabs to light, may be anticipated to the extent of stating that no evidence exists to show that blinded crabs react to light. The eyes therefore are the exclusive light receiving organs. The results with the blinded crabs show that

a tactile stimulus may initiate the decorating response. There is, however, no evidence to show that the tactile stimulus is the only stimulus adequate to produce this response. Whether visual stimuli alone may initiate such responses is as yet undetermined. Complete tactile anaesthesia would be necessary with vision unimpaired. Such an experiment is technically feasible and ought to be made forthwith.

Four crabs were used in this experiment. Specimen 7, a female, was blinded VIII–21–12 by cutting off the eye stalks close to the orbit by means of a pair of scissors. The animal was then placed in the aquarium. It manifested considerable restlessness by moving about the walls of the aquarium. It assumed a position in one corner of the aquarium from which it refused to move for some time. On VIII–28–12 this individual was found to be gaily decorated with ulva. These decorations were removed completely and on the next day, VIII–29–12, the animal was observed to be again decorated with seven or eight pieces of ulva which had been placed upon the legs and back of the carapace. The animal was observed from time to time until IX–6–12 when it was found to be covered with polysiphonia with only two pieces of ulva on the legs. The polysiphonia had been placed in the aquarium VIII–27–12. No other crab made use of this material for decoration. The polysiphonia was removed from this individual IX–6–12. Nothing had been added by IX–8–12, 12:30 P. M. The animal died IX–9–12.

Specimen 26, a young female, was blinded IX–7–12 at 4 P. M. by cutting off the eye stalks with a pair of scissors. All foreign material was then stripped off from the carapace and legs by means of a pair of forceps. Immediately following the operation the animal was very restless and made no attempt either to feed or to decorate itself or to preen. There was no decoration IX–8–12. On IX–9–12 the animal was observed to be covered with pieces of ulva and polysiphonia. The ulva was removed from the rostrum. A few minutes later the animal was observed to place a flag of ulva 18 mm. by 6 mm. on the rostrum after "mouthing" it. The animal was observed to feed on dead clam. On IX–10–12, 2:30 P. M., the animal was observed in the act of decorating itself. The manner of decora-

tion is precisely the same in the blinded crab as in those which have eyes.

Specimen 27, a female, was blinded by cutting off the eye stalks on IX–9–12. Her decoration, which consisted of green and brown algae was carefully stripped off with forceps. The crab was not so restless as Specimens 7 and 26. After the operation the animal remained still with the rostrum toward the side of the aquarium. On IX–10–12, 2:30 P. M., the animal was found to be decorated with polysiphonia and ulva. I observed her at work. She seized a bit of polysiphonia with both claws, tore off a small piece apparently stuffed it into, the "mouth," drew it forth with the right or left chela and placed the weed upon the carapace. If it did not stick the first time she repeated the operation. IX–11–12 the animal was found to be more completely decorated than before with ulva which was placed mainly upon the legs.

Specimen 28, a large male, was very elaborately dressed in green and brown algae with hydroids, small tunicates, sponges and tubeworm on its carapace. After carefully stripping off the decorations with the exception of the tubeworm that could not be removed, the eye stalks were clipped off close to the orbits, IX–9–12. The animal did not appear to be much disturbed. IX–10–12, 2:30 P. M., the animal was decorated with two or three large pieces of ulva upon the carapace. It was observed in trying to place a piece of polysiphonia on the carapace; the polysiphonia failed to stick. The animal did not repeat the operation. IX–11–12, placed a non-mutilated female in the aquarium with this male at 3:30 P. M. At 5 P. M. observed the two individuals copulating. They remained joined for 30 minutes. Called O's attention to them.

The conclusion of these experiments is identical with that reached by Bateson [10] and Minkiewicz.[11] Deprivation of the eyes affects in no particular either the series of acts by which the foreign bodies are applied to the animal's body or the appearance of the resulting decoration.

5. *The reaction of blinded crabs to light.*—In endeavoring to determine the sort of stimulus and receptor which causes the

[10] Notes on the Senses and Habits of Some Crustacea. *Jour. Marine Biological Association.* Vol. I, p. 211, 1889.

[11] Loc. Cit., p. 43. Les Crabes Aveuglés.

decorating response, recourse was had to the experiment of blinding the crabs. It became evident after the experiments, described in section 4 preceding, had been made that a tactile stimulus may serve as excitant to the response. The relation of the response to the visual and tactile stimuli may be represented by means of letters in order to throw more clearly into relief the logical implications of the experiments. Let V stand for the visual stimulus, let T stand for the tactile stimulus, let R stand for the decorating response. In the non-mutilated crab, when R occurs both V and T are present. There are three possibilities as to the relation between R, V and T. V alone may initiate R; T alone may initiate R; or V and T together may initiate R. The experiments with the blinded crabs seemed to show that T alone may initiate R. Whether V alone may initiate R remains to be demonstrated by producing some sort of tactile anesthesia in the legs and chelae without damaging motion. The experiments with blinded crabs seemed to prove beyond doubt that the tactile stimulus alone may initiate the response. Before such a conclusion is warranted, however, the possibility of light receptors other than the eyes must be excluded. It is conceivable that the integument of the crab may respond to light in some such way as does the skin of the frog. To eliminate by experiment this possibility, which indeed seems very remote, blinded crabs were placed in the reaction box and their behavior observed through the hole in the top. Specimens 7, 26 and 27 were used. Specimen 26 gave no reaction whatever when placed in the reaction box with red in the left, and yellow in the right, window. Specimens 7 and 27 wandered apparently aimlessly about the walls of the box without stopping in front of the windows. It seems certain, therefore, that blinded crabs do not react to light stimuli.

III. CONCLUSIONS

1. The color reactions of *Oregonia gracilis* are determined by the color of the light to which it has been previously exposed. This conclusion is justified by the results of section 2 of our experiments. The result may be explained by supposing that this crab possesses a specific chromo-kinetic resonance, or to state the same fact in other words, that it acquires a specific chromotropism. This acquired chromotropism may be as-

sumed to be dependent upon a specific modification of the light receptor organs and the nerve cells connected with them, which determines the kind of stimulus to which a crab possessing such a "resonance" can respond.

2. Blinded crabs decorate themselves as do normal crabs both as regards the mode of operation and the result.

3. Blinded crabs do not react to light stimuli. These latter results taken together show beyond doubt that some other than the visual stimulus may excite the decorating response. This other stimulus may be assumed to be tactile. The results, however, leave in doubt the question whether visual stimuli alone may excite the decorating response.

The results just stated are the only experimentally determined conclusions which may be drawn from our work. And the problem stated at the outset of the paper "By the action of what stimuli and by the execution of what responses is the decoration carried out" must remain unsolved for the present. Of the three possibilities enumerated on page 176 only two, namely, the second and the third can be definitely disposed of. The three possibilities were:

i. Visual stimuli alone may initiate the response.
ii. Tactile stimuli alone may initiate the response.
iii. Visual and tactile stimuli together may initiate the response.

Whether visual stimuli alone can initiate the response remains undetermined by our experiments. It might seem from the existence of a specific, acquired, chromotropism that visual stimuli may certainly excite the instinct in question. Such an assumption is actually made by Minkiewicz. But a moment's reflection will show that all that the chromo-kinetic resonance does is to move the crab fatally towards a source of light of the same quality as that to which it has been exposed. It is quite conceivable that such an acquired chromotropism has nothing whatsoever to do with the decorating instinct. Indeed it is only the belief that a "harmony" existed between costume and color environment that has jutified the assumption. Whether a crab deprived of tactile receptors yet possessing light receptors and impressed with a chromo-kinetic resonance would decorate itself when placed in the presence of suitable material is an unsolved problem. The writer is of the opinion that such an

animal would not decorate itself although he realizes that such a statement is merely an expression of individual opinion.

It seems very unlikely that acquired specific chromotropism is limited to *Oregonia gracilis*. Assuming that the facts stated in section 2 of this paper are confirmed by other workers, it is only reasonable to suppose that similar results will be found in other forms of life. If such a resonance is found to be widely distributed n nature, the co-existence in the same animal of an acquired chromotropism and a decorating instinct would be merely accidental and not causal. Proof by means of an *experimentum crucis*, of this assumed disconnectedness of the two phenomena in *Oregonia gracilis*, depends upon a tactile anesthesia in an animal with a demonstrated acquired specific chromotropism. If such a crab did not decorate itself, the hypothesis here suggested would be confirmed.

RESPONSES OF YOUNG TOADS TO LIGHT
AND CONTACT[1]

C. F. CURTIS RILEY

One figure

I. INTRODUCTION

Several years ago the opportunity arose to investigate the responses of a number of young toads, *Bufo americanus* Le Conte.[2] The toads averaged about 14 mm. in length. The animals were kept in a glass aquarium jar in the laboratory, the vessel being placed 3 m. from an east window in a shaded place. A piece of filter paper, dampened with water, was placed in the bottom of the jar in order to keep the animals moist. They were fed each day on small flies and mosquitoes.

As the toads displayed marked responses to light and contact, it was decided to commence experimentation with photic and contact stimuli. The entire series of experiments were carried on in a dark room at an approximate temperature of 22° C. For experimental purposes, a glass dish with parallel sides was used. The dimensions of the vessel were 60 x 25 x 6 cm., inside measurements. In order to eliminate the effects of reflection, the experimentation trough was painted a dull black on the inside with the exception of the two ends; each of which was covered with a strip

---

[1] Contributions from the Zoölogical Laboratory, University of Illinois, under the direction of Henry B. Ward, No. 21.

[2] The experimental work was done at Ann Arbor, Michigan, in the summer of 1904, and the first draft of the paper was made the following year. The literature was reviewed, the paper recast and entirely rewritten at Urbana, Illinois, during the winter of 1912-1913.

of paper having a dead black finish. This paper was so arranged that it could be readily removed at either end, thus permitting the rays of light to enter.

Unfortunately, the writer was unable either to complete the work on the responses to photic and contact stimuli, or to commence any experiments on other forms of reaction work. Through an oversight, the water was allowed to dry up in the jar containing the toads, and the next time they were needed for experimentation purposes they were found to be dead. As it was not possible, at the time, to obtain any more material, and as the opportunity to complete the work has not presented itself since then, it was thought best to publish in a brief form the results of the experiments incomplete as they are. The writer hopes, at some future time, to continue the work outlined in this paper in far more detail and to supplement it with experiments on responses to other forms of stimuli.

Thanks are due to Miss F. J. Dunbar of the Zoölogical Department of the University of Michigan, who kindly collected the amphibians used in these experiments. Mr. S. A. Rowland, of the Physics Department of the University of Illinois, calculated the intensity of the illumination within the field of experimentation employed in this work. His assistance is gratefully acknowledged. The writer also desires to express his appreciation of the criticisms and encouragement given by Doctor C. C. Adams of the University of Illinois.

II. RESPONSE TO INTENSE ARTIFICIAL LIGHT

The first experiments undertaken were with reference to intense artificial light as a source of stimuli. The light employed for this reaction work was obtained from the electric arc of a Thomson " 90° carbon " projection lantern. The current passed from the electric lighting circuit through a rheostat, and from there to the lantern. The current was direct with an approximate voltage of 210. Within the field of experimentation the illumination was approximately 10,000 ca. m. In order to eliminate the effect of the heat rays, the light was allowed to filter through a cell containing distilled water. Having placed the toads in the glass dish, it was then moved into the beam of light that emerged from the lantern. In order to prevent the organisms from becoming unnaturally dry during

experimentation, the trough was immersed in cool water from time to time, thus keeping the vessel cool and moist.

When the dish is placed in the beam of light, it is noticed that the toads are scattered promiscuously throughout the entire length of the vessel. The first demonstrative movement is a decided orientation. All the animals that are facing the light immediately turn around until their heads are pointing directly away from the source of illumination. The orientation is of such a nature that the longitudinal axes of their bodies become parallel with the rays of light. Those individuals which are facing away from the source of illumination, in the first instance, are already commencing to jump away from the light. After all the toads have completed the orienting reaction, there is a general movement towards that end of the dish farthest from the source of light. The animals jump rapidly toward the extremity of the vessel. The pauses between the jumps are very brief, in many instances barely extending over a second of time. Orientation with the longitudinal axis of the body parallel with the incoming rays is retained while the organisms travel the entire length of the dish. After reaching the end of the receptacle, the toads usually remain oriented with their heads touching the glass. If they are left in this position for some time, many of the individuals climb up the perpendicular end of the vessel as if to move away as far as possible from the source of illumination. Those that climb to the top are not in the most intense glare of the projection lantern, their elevated position placing them a little above the strong central beam of light. Possibly this movement may be due, in part, to response to contact stimuli. The dish is now turned around until the end where the animals are congregated is again brought nearest to the light. Those animals clinging to the upright end of the vessel quickly drop to the bottom. All the toads promptly perform the reaction of orientation and jump rapidly to the far end of the trough as in the former instance. This reversing of the dish is continued for about eight trials and the animals respond promptly each time to the photic stimuli, the response being as previously described.

Some experiments on the influence of intense light upon the swimming responses of the young toads were also undertaken.

Water with a temperature approximately of 22° C. is poured
into the glass receptacle to a depth of 4 cm. The animals are
then placed in the water and the vessel moved into the beam of
light emerging from the projection lantern. The organisms
immediately orient themselves with the longitudinal axis of the
body parallel to the rays of light. Complete orientation is
quickly followed by every animal swimming vigorously away
from the source of illumination to the extremity of the dish.
The young toads retain their precision of orientation as they
move through the water for the entire length of the vessel.
After all the animals have assembled at the end of the dish, it
is turned around, thus placing the organisms again nearest the
source of light. The animals as before respond promptly, swim-
ming to the far end of the vessel. In this connection it may be
mentioned that Torelle (1903, p. 473) while engaged with some
very interesting experiments, demonstrated that in water *Rana
virescens* and *Rana clamata* move to the illuminated end of a
glass trough. Diffuse daylight was used in these experiments.

Many consecutive experiments of the nature of the above
were performed, the toads orienting themselves each time in
such a manner that the long axis of the body becomes parallel
to the rays of light; and they swim away from the source of
illumination as already explained. Frequently after reaching
the extremity of the glass trough, many of the toads climb up
its perpendicular wall. Attention has been drawn to this move-
ment in connection with the responses out of water. The ani-
mals respond as if they are attempting to recede as far as pos-
sible from the source of stimulation. When the end of the
dish, where the toads are congregated, is placed next to the
light, they very promptly drop off the perpendicular glass wall
into the water. Sometimes there is an attempt at orientation
even before leaving the wall of the trough for the water. The
results of the experiments in connection with both the jumping
and swimming responses of young toads differ, decidedly, from
the results of Parker's (1903, p. 29) suggestive work on *Rana
pipiens* Schreber. He found that these animals were positively
phototropic in light, from a Nernst lamp, even at 20,480 ca.m.
Without regard to the side of the frog that was exposed to the
light, they turned and jumped toward its source. The frogs
oriented themselves until they faced the source of illumination

and they remained in this position although the light was entirely unbearable to the human eye.

In connection with the responses of young toads both.in and out of water, it would have been extremely interesting to have used a much longer experimentation trough in order to demonstrate whether or not the animals were seeking a certain optimum intensity of illumination. The writer planned to perform experiments of this nature if more material had been available at the time, and he hopes to do so in the future.

In connection with these responses of young toads to intense light, it is of interest to recall the work of Pearse (1910) relative to frogs and toads. This writer (*l.c.*, p. 175) found that *Rana clamata* moved toward a light of 225 ca.m. from a six-glower Nernst lamp. Five specimens were subjected to the light. He also states (*l.c.*, pp. 175–176) that *Rana sylvatica* was exposed to photic stimuli from a light of the same intensity. His results are summed up in the following quotation (*l.c.*):

"This frog was more active than the last species, [*R. clamata*] and some individuals gave more decided phototropic reactions than did any member of the preceding species. There were, however, such differences in the reactions of the four animals used that they are tabulated separately. Individual No. 1 never failed to move straight toward the light. No. 2 was not as persistently positive after the eyes had been excised as before this operation, though it continued to give a majority of positive reactions. As individuals 3 and 4 were apparently indifferent to the light in their normal conditions, their eyes were not removed. The reactions of animals 1 and 2 were, however, strongly positive, and this condition remained even after the eyes had been excised; hence their skins served as photoreceptors as well as their eyes."

These results with frogs are quite, different from the results of the writer with young toads. Such differences, however, are not at all surprising when it is recalled that not only are animals of different genera being considered, but also of different families; and further it must be kept in mind that on the one hand mature organisms are under observation and on the other very immature ones. Pearse (*l.c.,*. p. 176) also experimented with *Bufo americanus* and *Bufo fowleri*. The records of the two species were not kept separate. The toads respond positively to a light of 225 ca.m., moving toward the source of illumination. Most of the animals used were adults, but a few were immature. None of them, however, were less than 2 cm. long. It has been demonstrated that the present writer finds young toads to respond negatively to the light from a projection lantern. The

difference in these results from those of Pearse is probably due to the fact that the writer employed more powerful stimuli in his experiments. Further, the writer used animals of much greater immaturity than was the case in Pearse's experiments.

III. RESPONSE TO LESS INTENSE ARTIFICIAL LIGHT

The young toads are next subjected to light of much lower intensity. The vessel containing the animals is placed directly in front of the bulb of an ordinary 16 c.p. incandescent electric light. Within the field of experimentation the illumination is approximately 44 ca.m. The first noticeable movement is the orienting response, all the toads so placing themselves, with respect to the light, that the longitudinal axes of their bodies become parallel with the longitudinal axis of the dish, which points directly toward the light. This response brings the toads into such a position that their heads are turned directly toward the source of illumination, and the median longitudinal axes of their bodies lie parallel with many of the rays passing through the bulb. However, with a light of this nature, it is incorrect to state, without qualification, that the median longitudinal axis of the body is parallel with the rays of light. Immediately after completing orientation, the toads jump in the direction of the light until they all reach the extremity of the vessel nearest to the source of illumination. The organisms remain oriented while traveling from one end of the glass trough to the other. Parker (l.c.) found that Rana pipiens Schreber oriented itself with its head toward the light and also moved toward the source of illumination. These were the responses to the intermediate light intensities between 1 and 20,480 ca.m. After the young toads had all reached the end of the vessel, it is turned around until the animals are moved to a position farthest from the source of light. They quickly perform the orienting response and again jump away toward the light. In this manner the animals are driven repeatedly from one end of the dish to the other. Usually, orientation is not performed so promptly nor do the toads jump so rapidly as in those experiments with the projection lantern. When the animals reach the end of the trough, they frequently climb up the end wall of the vessel as if to move still nearer to the source of illumination. There is no definite evidence that the median longitu-

dinal axes of the toads lie parallel with all the rays of light, for the rays emerge from the bulb at various angles and many of them must cross within the area of experimentation.

These results seem to indicate that young toads respond positively to incandescent light of 16 c.p. They orient themselves in such a manner that the long axis of the body lies parallel to some of the incoming rays and the head is turned directly toward the source of light. They retain this orientation with considerable precision while traversing the entire length of the experimentation dish. The fact that the animals move as near as possible to the light, and in some cases climb to the top of the glass wall at the end of the vessel, leads one to infer that the intensity of the light is a factor in causing the movements, rather than the direction of the rays *per se* in the field. In connection with the experiments on young toads just described, it is interesting to compare the work of Parker (*l.c.*) on *Rana pipiens* Schreber. He noticed the interesting fact that,

> "With the lower intensities the animals often did not react for from five to ten minutes or even longer, and the jumping response was frequently omitted; but their orientation was finally always with their heads toward the source of light, that is, positive. In some instances after a frog had remained ten minutes or more without changing its original position, it was induced to jump by being touched from behind, and, when this was done, the animal almost invariably turned first and then jumped toward the source of light."

It has been demonstrated that stimuli from a 16 c.p. incandescent electric light affects young toads in much the same manner as Parker has observed with reference to frogs. The toads orient more slowly to the weaker light than to the stimuli from the projection lantern. Movement toward the incandescent light is also more deliberate than toward the light from the projection lantern.

Dickerson (1906, p. 66) also has noticed that toads respond positively to artificial light of relatively low intensity. Her statement is as follows:

> "If we go to a pond at night, we shall have every opportunity both to see and hear toads, especially if we carry a lantern. Instead of being frightened by the light, they are attracted by it and may gather about it. If the lantern is set on the ground, they sometimes try to climb to its top."

The results of my experiments with less intense artificial light agree very largely with those of Cole (1907, p. 392) on *Acris gryllus* Le Conte. This observer states that the source of the

photic stimuli was an electric light situated 50 cm. above a
flat surface on which the frogs were placed. *A. gryllus* faces
the source of illumination and leaps toward it. When a frog
jumps past the light, the animal remains with its back turned
toward it for a short time. Then it turns in such a manner
as to face the light and again leaps toward it. Cole (*l.c.*, pp.
393–401) also found that both *A. gryllus* and *Rana clamata*
Daudin respond positively to light with an intensity of from
1.25–5 ca.m. by turning toward the source of illumination, but
that individuals of the latter species were much the slower in
their responses. He noticed that the positive response of *A.
gryllus* occurs more quickly and uniformly when light of 5–20
ca.m. is used. This is in accord with the present writer's ex-
periments on *Bufo americanus* as it is also in accord with the
results of Parker (l.c.) with *Rana pipiens* Schreber already
mentioned. It should be stated that during these experiments
of Cole with *A. gryllus* and *R. clamata*, the animals were con-
fined in glass boxes which were of such dimensions that the
amphibians could turn readily in any direction, but were unable
to jump away. My experiments are also essentially in agreement
with those of Mast (1911, p. 219–220). This worker subjected
seven toads to light from a single source. Two intensities were
used, one of 12.5 ca.m. and the other of 25 ca.m. Five of these
toads were small ones, but the exact size is not given. The
following quotation presents the results which have more direct
bearing upon the experiments described in the present paper:

> "They all oriented directly· and fairly accurately. If placed on the
> table in the beam of light so that one side faced the glower they turned
> slowly but directly until they faced the light and then hopped or walked
> toward its source, stopping frequently for a few moments at intervals
> on the way. * * * The toads always went directly toward one or
> the other of the two sources."

IV. RESPONSE TO STRONG DIFFUSE DAYLIGHT

It was found that young individuals of *Bufo americanus*
respond to diffuse daylight of relatively strong intensity, and
a number of experiments were performed in which light of this
nature was employed. The glass trough containing the toads
was placed on a table, having a black surface, at a distance
of 50 cm. from an east window. A glass plate, painted a dead
black on the under side, was placed over the top of the experi-
mentation dish. Then the strip of black paper, covering the

end of the vessel facing the light, was removed. Such an arrangement modified, considerably, the effects of the cross rays.

It is noticed, after the dish containing the toads has been near the window for a few seconds, that the animals orient themselves with their heads toward the source of light and with the long axes of their bodies parallel with the longitudinal axis of the vessel used for the reaction work, but not parallel with the great majority of the rays, for these enter the dish at various angles notwithstanding the precautions already described. The toads jump away in a comparatively straight line toward the light. All the organisms are soon congregated at the end of the trough nearest to the window. Not infrequently some of them climb up the glass wall at the end of the dish and cling in that position. The vessel is turned around until the end where the toads are gathered is pointing directly away from the window. Those that are clinging to the glass side drop down to the floor of the trough. All the animals again turn their heads toward the window and move off, with the long axes of their bodies parallel with the longitudinal axis of the experimentation dish, in the direction of the source of illumination. In a short time they are all found at the extremity of the vessel. Experiments of this nature are continued for eight successive trials. Each time the animals move promptly from one end of the dish to the other. As in the experiments with incandescent electric light, there is evidence that orientation does not occur quite so promptly nor is locomotion so rapid as in the experiments with the projection lantern.

These experiments appear to indicate that young toads respond positively to diffuse daylight of somewhat strong intensity. They also exhibit definite orientation with the anterior end of the body turned directly toward the light. But it cannot be said that the long axis of the body lies parallel to the incoming rays, for it is evident after careful consideration that these must enter the experimentation trough at many and varied angles, numbers of them passing, more or less, along its entire length.

The responses of toads and frogs to strong diffuse daylight have been observed by other workers, and a brief comparison will be made with the results of some of their experiments. It is of interest to notice that, Graber (1884, p. 124) found that toads, *Bufo vulgaris* Laur, placed in a box with two compart-

ments, one of which was darkened and the other exposed to diffuse daylight, moved toward the darkened compartment and tended to collect there. According to Graber's (*l.c.*, pp. 39, 40) description of his own methods used in experimentation, the natural inference is that he used strong diffused daylight as a source of stimulation, except in those instances where it is stated specifically otherwise. The following quotation presents his results (*l.c.*):

> "Da die meisten Versuche, die ich mit diesen ekelhaften Tieren anfieng, ein negatives Resultat ergaben, glaubte ich mich in eine genauere Licht-gefühl-Prüfung nicht einlassen zu sollen und geh' ich auch bei der Mitteil-ung der erhaltenen Reactionswerte ganz summarisch zu Werke.
>
> "Aus der Vergleichung von Weiss und Schwarz geht zunächst hervor, dass, wie zu erwarten war, die dunkle Abteilung der hellen bei weitem vorgezogen wird.

$$\text{``1)} \quad \frac{\text{Weiss}}{\text{Schwarz}} = \frac{1}{8.4}.$$

> "Darnach ist also die Lichtscheu der Kröte (obiger Quotient beruht freilich nur auf 5 aber unter sich übereinstimmenden Beobachtungen) entschieden viel grösser wie jene des Frosches (aber kleiner wie die des Triton)."

While it is evident that the results of Graber's experiments differ from those of the writer, yet attention should be drawn to the fact, as indicated in the first paragraph quoted, that there was evidently some doubt in the author's mind as to the correctness of his own results. Plateau (1889, p. 82), however, working with *Rana temporaria* and *Bufo calamata* reached conclusions of an opposite nature. He demonstrated, when specimens were liberated in an experimentation box lighted by windows at one end only, that both specimens responded positively to the light and jumped toward the source of illumination. One infers from Plateau's (*l.c.*, p. 81) statement that strong diffuse daylight was used in his experimental work with amphibians. According to Loeb (1890, p. 90) frogs respond negatively to strong diffuse daylight. Torelle (1903, p. 469) experimented with *Rana virescens virescens* and *Rana clamata* and demonstrated that both species oriented in such a manner that their heads pointed toward the source of illumination, diffuse daylight, and also that they moved toward the light. Dickerson (*l.c.*, p. 32) states that the frog moves toward diffused light, probably meaning strong diffuse daylight.

V. RESPONSE TO WEAK DIFFUSE DAYLIGHT

A number of experiments were performed with weak diffuse daylight. The light was obtained from a south window. The incoming rays passed through a small slit-like opening in the wall of the dark room before reaching the experimentation dish. The length of the opening corresponded with the width of the vessel and the width of the former was equal to the depth of the latter. The window through which the light entered was 4 m. distant from the dark room (see Fig. 1, A).
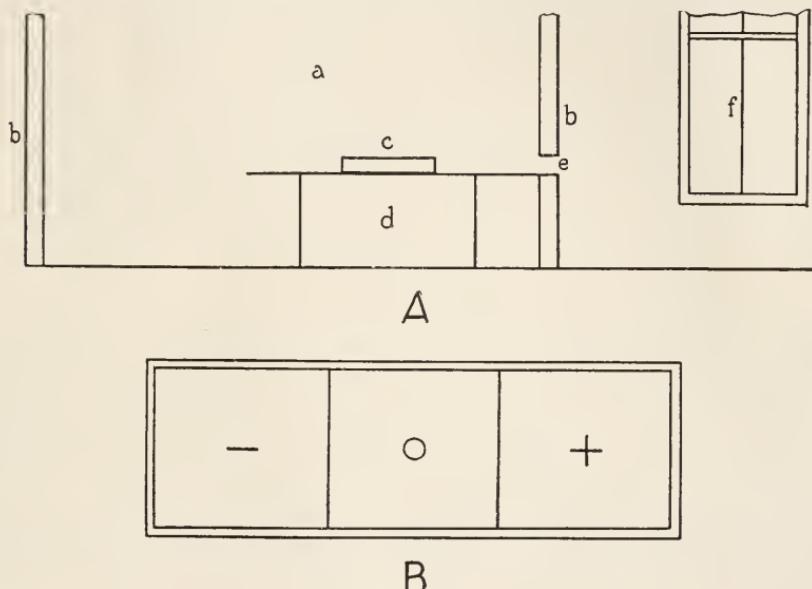
FIGURE 1. A. Sectional diagram showing plan of apparatus employed in testing responses of young toads to stimulation from weak diffuse daylight. B. Experimentation dish enlarged more than is shown in A. a, Interior of dark room; b, walls of dark room; c, experimentation dish containing young toads; d. table; e, opening through which light enters dark room; f, window through which light enters, situated in wall of outer room; +, positive; —, negative; 0, indifferent. (Not drawn to scale.)

The glass trough containing the toads was placed in close proximity to the slit-like opening. It was noticed that there was no immediate response to the light, neither by orientation nor by movement toward or away from the source of illumination. This being the case observations were taken every fifteen minutes, and the positions of the animals in the dish noted. The

vessel was divided by transverse lines into three equal divisions (see Fig. 1, B). Toads found in the section marked + were considered to respond positively to the light. Those gathered in the division marked — were enumerated as responding negatively. The organisms congregated in the space marked o were counted as being indifferent to the illumination. Table I indicates the results of six experiments with twelve individuals used in each experiment.

TABLE I

Responses of Young Toads to Weak Diffuse Daylight

Number of Experiments	Positive	Indifferent	Negative
1	7	2	3
2	6	1	5
3	8	2	2
4	6	2	4
5	7	1	4
6	8	2	2
Totals	42	10	20

The above table shows that out of a total of 72 responses, 42 of them may be considered as being positive, 20 as being negative, and 10 as being indifferent. The writer performed many other experiments beside those indicated in Table I, some of which showed a rather higher percentage of positive responses than evidenced in the table; but it is believed that the results indicated there present a fairly representative series. From these results the inference is drawn that young toads respond positively to weak diffuse daylight. However, the orientation of the animals lacks the definiteness exhibited in the experiments with light of stronger intensities. Neither the motor response nor the orientation is so precise as is the case in the experiments with strong diffuse light. Many of the toads that collected in the section marked + faced the slit-like opening in the wall of the dark room through which the light entered. Those toads that faced the light have the median longitudinal axes of their bodies parallel with the longitudinal axis of the experimentation dish and also parallel with a portion of the incoming light rays. But it must be remembered that the rays cross at many and varied angles, and while it is true that

many of these cross lights are cut out as the rays enter the dark room, yet it would be incorrect to state that all the rays of light are parallel with each other and with the median longitudinal axis of the bodies of the toads facing the light.

Graber (*l.c.*, pp. 120, 121) while making observations on *Rana esculenta L.*, stimulated by means of weak diffuse daylight, "meist trüber Himmel," states results which lead to the inference that these animals react negatively to photic stimuli of such a nature. However, their responses were not so preponderantly negative as was the case of *Bufo vulgaris* Laur already mentioned. The following quotation will give an idea of his results (*l.c.*, p. 121):

> "Auch zeigt der Versuch, dass das Reactions-Verhältnis ein sehr constantes ist, indem die Weiss-Frequenz sich zwischen 11 und 18 und die des Schwarz zwischen 22 und 29 bewegt, und grössere Extreme, wie solche sonst sehr häufig sind, mit Ausnahme eines einzigen Falles (7:33) gar nicht vorkamen.
>
> "Das Mittel-Verhältnis ist:
>
> $$1) \quad \frac{\text{Weiss}}{\text{Schwarz}} \quad \frac{1}{1.5} = \text{.''}$$

Loeb (*l.c.*, p. 89) experimented with frogs subjected to weak diffuse daylight, and found that they responded by moving away from the light.

VI. RESPONSE TO SUNLIGHT

No systematic experiments were undertaken in order to determine the effect of sunlight on the behavior of young toads. However, a few incidental observations were made and these were recorded.

The young toads were kept in a large glass aquarium jar when not under experimental observation. This chanced to be placed near a window with an eastern exposure. A narrow beam of sunlight entered the dish, and to one side of these rays of bright light was diffuse daylight. The animals jumped toward the side of the jar at which the sunlight entered. Usually they remained in the sunlight for some time. This response seemed to vary, for certain individuals remained in the direct light longer than others. However this may be, there was certainly a response to sunlight, evidenced by the toads jumping toward the window where the sunlight entered. Frequently the animals were found in the less illuminated portions of the jar,

but they usually remained at the side of the vessel nearest to the window. On sunny days the writer often has observed that young toads respond both to moving shadows and moving objects. Sometimes they respond by crouching against the ground, and at other times by the jumping response. The response to moving objects has been noticed also on cloudy days. The writer did not employ a heat screen during any of these observations. Therefore there was no definite attempt to isolate possible temperature responses from photic responses. However, he infers from the experiments of Pearse (*l.c.*, pp. 192–195) that these responses are probably not due to temperature. My observations were recorded in the middle of the day, during the month of July. Similar responses occurring in the early spring or late fall may be due largely to temperature.

Torelle (1903, p. 469) working with *Rana virescens virescens* and *Rana clamata* noticed, in one series of experiments, that specimens of both species responded positively to sunlight, but that they did not stay in the circle of most intense illumination. Some individuals moved away without turning. Others turned and retreated some distance, and then oriented themselves with their heads pointing toward the incoming beam of sunlight. In another series of experiments in which specimens of the same species of frogs were placed in a box, admitting sunlight at one end and diffuse light at the other, Torelle (*l.c.*, p. 471) found that the animals "turned toward and moved to the end" where the sunlight entered. They did not stay within the area of strongest light, for they either moved to the opposite end of the box, or else backed, without turning, into the region where the light was less intense. These results correspond more or less to my observations on young toads; although unfortunately the present writer did not observe the kind of response when the animals moved into the less illuminated area. Dickerson (*l.c.*, p. 71) has noticed the response of young toads to sunlight. She states that, "They congregate in large numbers on sunny brown earth patches." Such places are near or among the grass. The observations of Miller (1909, pp. 659–660) are in accord with those of Dickerson. The former has noticed that toads are rarely seen during the day unless it is cloudy. Late in the fall, however, they are found in the sunlight, among the grass. It should be stated that none of these

writers, Torelle, Dickerson and Miller, indicate clearly whether the response is due to light or temperature.

VII. RESPONSE TO COLORED LIGHT

A few experiments of a very general nature were performed with colored light as the source of stimulation. The young toads were subjected to the stimuli from a 16 c.p. incandescent light. At first the light was passed through glass of various colors. Later the rays were transmitted through colored solutions prepared according to the directions recommended by Nagel (1898, pp. 649–655). Such light proved to be more nearly monochromatic, as was seen on examination with the spectroscope. The solutions were placed in a glass cell with parallel sides. Red and blue are the only colors that will be referred to here.

The young toads are seen to be scattered promiscuously throughout the experimentation dish when it is placed in the beam of light transmitted through the red solution. Frequently there is observed to be considerable hesitancy before the animals orient themselves with reference to the light. Some of them turn toward the light, while others exhibit no definite orientation. In some experiments it is observed that the number of toads responding positively to the light is slightly in excess of those responding negatively; but in other experiments the reverse proves to be the case, for the number of animals exhibiting the negative response to the light is somewhat greater than those exhibiting the positive response. Usually, however, it may be stated that a small majority of the toads turn in such a manner that their heads point toward the source of illumination. Some animals orient a few seconds after they are placed in the beam of light. Others wait much longer than this before they turn either away from or toward the red light. Certain individuals jump in the direction in which their heads are pointing, immediately after orientation is completed, while others wait from a few seconds to several minutes before they jump away. The jumping movement toward the red light is far less common than is the case with reference to the blue light. In general it may be said that the movements of young toads away from and toward the source of illumination are slower and with more and longer pauses between the jumps than is the case when

white light is used. It is evident that red light is not a very effective form of stimulus, certainly the toads are not nearly so responsive to it as they are to white light.

In the experiments with blue light the toads are observed to be distributed at various different points in the experimentation dish. This is placed in the beam of light emerging from the blue solution. The animals turn with promptness toward the source of illumination. In most cases they jump immediately toward the light, or with a delay of but a few seconds. There are comparatively few pauses between the jumps and these are of short duration. Not only is the orienting response more prompt, but the movement toward the light is also more vigorous than is the case when the red solution is used. The orientation of the toads and their movement toward the source of illumination are very similar to the results observed with the 16 c.p. incandescent light when neither the red nor the blue solution is used.

Torelle (*l.c.*, p. 478) found when single colored lights were used that specimens of *Rana virescens virescens* and *Rana clamata* always jumped in the direction of the blue light and remained with their heads pointed toward it, touching the glass. On a frog being placed close to the red light, it usually turned away from the source of illumination. In some cases the animal not only turned, but jumped away from the red light. When a frog was placed about 30 cm. away from the red light, the animal generally remained there and did not jump toward the light. According to the experiments of Pearse (*l.c.*, p. 189) with *Rana palustris*,

"The results show that the blue is apparently the most effective in the production of positively phototropic reactions, and that there is a regular graduation from blue to red, both in the percentage of positive reactions and in the rapidity with which the movements took place. * * * It is probable that these differences in the reactions are due to differences of the wave lengths, but they may be due to intensity differences."

These results of Pearse with *R. palustris* are largely in accord with those of the writer with young toads. Results similar to those of the writer on young toads when blue and red lights were used were obtained by Laurens (1911, p. 267). He subjected *Bufo americanus* and *Bufo fowleri* to the stimuli from single monochromatic lights of equal intensity, using Nernst

glowers for the source of illumination, and showed that members of both species reacted by giving motor responses, turning and jumping toward or away from the light. In one series of experiments with blue light, there were 251 positive responses and 37 negative ones. In another series of experiments with red light, there were 167 positive responses and 121 negative ones. The former series shows the percentage of responses to be 87 positive to 13 negative, while the latter series shows the percentage of responses to be 58 positive to 42 negative.

"By way of summarizing the results of the experiments with single monochromatic lights in which both the eye and the skin acted as receptors, it may be stated that all four colored lights used produced positive responses. Blue light was the most effective, and the other lights formed a decreasing series, corresponding roughly to their relative position in the spectrum, the red light being but slightly more effective than darkness." (Laurens, l.c.)

This summary presents results which are in extremely close agreement with those of Pearse (l.c.) on Rana palustris.

Some observations were recorded when stimuli from light of different colors, red and blue, were impinging upon the toads at the same time. The glass vessel containing the animals was so placed that the red light was situated at one extremity and the blue light at the other. The position was such that one end of the dish was in the beam of red light and the opposite end in the beam of blue light.

The young toads are placed in the center of the dish, approximately half way between the lights passing through the red and blue solutions. There is little more exhibited in the resulting responses than has already been recorded with reference to the single colored light. Orientation and movement toward the blue light are more definite and more vigorous, than they are with respect to the red light. By far the majority of the animals jump toward the blue light. A few individuals jump toward the red light. These make longer pauses between the jumps than is the case of those toads moving toward the blue light. Frequently periods three minutes or more in duration elapse between some of the jumps. At times one or two specimens appear to be indifferent to either light. In several instances observations were recorded after a period of fifteen minutes from the time the toads were first placed in the experimentation dish. In these experiments twelve toads are used each

time. Table II indicates the position of the toads with respect to the two colored lights for four sets of observations.

TABLE II

RESPONSES OF YOUNG TOADS TO COLORED LIGHTS

Experiment	Blue	Red	Indifferent
1	10	2	0
2	7	3	2
3	10	1	1
4	9	2	1
Total No. of Responses	36	8	4

It is seen from the table that out of a total of 48 responses, 36 are toward the blue light, 8 are toward the red light, and 4 are indifferent, apparently being no response to either of the colored lights. The blue is evidently by far the more effective color with respect to the responses of young toads when stimuli from both red and blue light are impinging upon them.

The results recorded above are largely in accord with those of Graber (*l.c.*, p. 125) on *Bufo vulgaris* Laur as indicated in the following quotation (*l.c.*):

"Dass auch bei diesen Reactionen wieder in erster Linie die Helligkeits-verhältnisse ausschlaggebend sind, geht schon aus dem Umstande hervor, dass einerseits Dunkel-Rot, andererseits Dunkel-Blau vorgezogen wird. Speciell aus der ersten Vergleichung, wo Rot sehr bedeutend dunkler als Blau und doch nur wenig stärker als letzteres besucht ist, könnte aber vielleicht geschlossen werden, dass diese Farbe als soloche der Kröte weniger angenehm als Blau sei. * * *

$$2) \quad \frac{\text{Rot}}{\text{Blau m. uv.}} = \frac{1}{1.2} \quad ?"$$

While it is true that in one series of experiments when "Dunkel-Rot" and "Hell-Blau" lights were employed, the number of responses were 305 toward the former and 288 toward the latter, or in proportion of 1 : 0.9, yet in another series when "Hell-Rot" and "Dunkel-Blau" were used, the responses were 108 to 142, or in the reaction-proportion of 1 : 1.3. Graber (*l.c.*, p. 122) experimenting with *Rana esculenta* L. obtained results somewhat at variance with those of the writer on young toads. The lights employed were "Hell-Rot" and "Dunkel-Blau." Three sets of experiments were performed, each con-

sisting of ten trials. There were 736 responses toward the red and 464 toward the blue. The following quotation gives a brief statement regarding the experiments (l.c.):

"Da Rot, trotzdem es heller als Blau war, in 30 Fällen 26mal stärker als letzteres besucht wurde, unterliegt es wol keinem Zweifel, dass dasselbe dem Frosch, ähnlich wie dem Triton, viel angenehmer als das Blau ist. * * *

"Als (Minimal)-Verhältnis ergibt sich

$$2) \quad \frac{\text{Rot}}{\text{Blau m. ult.}} = \frac{1}{0.6}.$$

d. h. es kommen auf 10 Rot- durchschnittlich nur 6 Blau-Besuche."

The results of Graber's experiments with *Rana esculenta* L., according to Torelle (*l.c.*, p. 487),

"Can be explained only on the ground of a confusion arising as a result of using so many frogs (forty) at the same time in one receptacle."

As will be shown, Torelle (*l.c.*, pp. 478, 479) obtained results with frogs, *Rana virescens virescens* and *Rana clamata*, exposed to the stimuli of red and blue lights both at the same time, much at variance with those of Graber (*l.c.*). For experimental purposes Torelle used a low, narrow box about 45 cm. in length with a glass plate at each end. Red light was admitted at one end of the box and blue at the other. The frog was then submitted to the influence of the two lights. The response toward the blue light was immediate, the animal moving toward the source of illumination. Frequently the frog remained with its head against the glass and turned toward the light. Apparently there was no movement on the part of the frogs toward the red light. These results of Torelle's with frogs are largely in agreement with those of the writer with specimens of young *Bufo americanus*, as they are also with the statements of Holmes in regard to frogs. According to this author (1907, p. 349) the blue and the violet rays are the most effective in producing phototactic responses. When two lights are used, red and blue, frogs collect near the blue light.

The results of the writer with specimens of young *Bufo americanus* and those of Laurens (*l.c.*, pp. 277–282) with *Bufo americanus* and *Bufo fowleri* are in accord. He worked with pairs of balanced colored lights and found that the toads reacted by giving motor responses, either jumping toward or away from the source of illumination. The animals also responded by

orienting themselves so that their heads pointed toward or away from the light. In one series of experiments with red and blue lights, out of a total of 960 responses, 788 were toward the blue light, 167 were toward the red light, and 5 were indifferent. Viewing the responses from the percentage basis, 82 per cent were in favor of the blue light, while only 17 per cent were in favor of the red light. It will be noticed that the results in the main are similar to those obtained with single monochromatic lights. However, it should be stated that the responses were not quite so quick as was the case with single lights. There were movements toward both lights, but those toward the blue far outnumbered those toward the red.

"It cannot be said that there is much evidence in favor of positive phototropism for the red light." (Laurens, *l.c.*, p. 280.)

In comparing these experiments of Laurens, with balanced blue and red lights, with those of Pearse (*l.c.*) on *Rana palustris* with single blue and red lights, it is of interest to observe that the results in the two cases very largely agree, in that there is a greater number of positive responses toward the blue light than there is toward the red light. However, it should be noticed that there is a much larger percentage of positive responses with reference to the blue light in the former's experiments with balanced blue and red lights, than is found to be the case in Pearse's experiments with blue and red lights used singly. It should also be noticed that in Pearse's experiments the results indicate many responses that were indifferent with respect to the red light.

VIII. RESPONSE TO CONTACT

Some observations were made on young specimens of *Bufo americanus* with reference to their responses to contact stimuli. While no systematic experiments were undertaken in order to study the effect of contact on the behavior of the animals, yet certain incidental observations were recorded. Some data were obtained regarding the influence of contact stimuli on the response to light. Record was made of observations on a form of a contact response resembling the death-feint among Arthropods. Some description also was given of the work of other writers with regard to the contact responses of toads and frogs.

During the experiments with light there were usually a num-

ber of young toads in the experimentation dish at the same time. Occasionally in jumping toward or away from the source of illumination two individuals come in contact with each other. Frequently this contact appears to have no effect upon the animals so far as their response to light is concerned. At other times one or both of the toads pause for a few seconds before again reacting with the motor response with reference to the light. Generally, however, when contact occurs it seems to act as a stimulus in inducing the motor response. This is noticeable when a toad, in jumping, comes in contact with a stationary individual, the latter's motor response being invoked. If a toad does not respond to the light for a few seconds, but remains quietly resting in one position, and if then it is stimulated by means of another animal jumping against it, the motor response may result and this may be followed by the animal responding to the photic stimuli. These statements apply more largely to the experiments with the weaker intensities. Parker (*l.c.*, pp. 28, 29) found when subjecting frogs, *Rana pipiens* Schreber, to the lower light intensities from a Nernst glower that,

> "In some instances after a frog had remained ten minutes or more without changing its original position, it was induced to jump by being touched from behind, and, when this was done, the animal almost invariably turned first and then jumped toward the source of light."

Pearse (*l.c.*, pp. 177, 178) in discussing "the influence of mechanical stimulation on the photic reactions of the toad," *Bufo americanus* and *Bufo fowleri*, when subjected to a light intensity of 220 ca.m. states that,

> "In jumping about they stimulated each other in a mechanical way. * * * It is evident * * * that mechanical stimulation exerts an influence on the phototropism of the toad by enforcing the effect of light, or, it could perhaps better be said, that the mechanical stimulation furnishes the *impulse* to locomotion, while the light is effective in *determining* the direction of the movement after locomotion has been established."

The writer has noticed in his experiments with the less intense illuminations that when several young toads move into the angles formed by the bottom and sides of the experimentation dish that the contact of their bodies and of the solid surfaces of the vessel seem to inhibit the motor response for some time. The animals remain quietly resting with their bodies in rather close contact. During the experiments with weak diffuse daylight, it was found that when stones were placed about 25 mm. apart

in the experimentation dish that there was a tendency for some of the toads to move into the spaces between the stones. The writer has frequently observed a similar "habit" on the part of mature and partially mature frogs. Large numbers of frogs, chiefly *Rana pipiens* Schreber, were kept in two large tanks in a basement room, the tanks being in diffuse daylight. It was a very common sight to find as many as thirty individuals crowded closely together in the angles formed by the sides and bottom of each tank. Frequently they were congregated in the more shaded corners, and the taking of such positions might be due in part to a response to light. However, they were sometimes observed to be gathered in corners that were not so shaded. At other times frogs were found to be grouped in the corners of the tanks, both in shaded and unshaded situations. Not infrequently frogs were observed to be distributed sparsely about the more central and open portions of the tanks. Such groupings as have been described are in all probability due to responses to contact stimuli. The movement into the shade may be due in part to vision as Torelle (*l.c.*, p. 470) has suggested.

Other writers have recorded observations on the contact responses of toads and frogs. Torelle (*l.c.*, p. 477) experimented with specimens of *Rana virescens virescens* and *Rana clamata* in a jar of water and found that the propensity of the frogs to place themselves in contact with solid bodies "is apparently stronger when the temperature is lowered." The following interesting facts are quoted from the author's work cited above:

"When a rock was lowered into the jar in such a way that a small space was formed between it and the wall of the jar, the frog crawled into this space and remained there. When a space was formed between the bottom of the jar and the rock, it crawled into that. This was tested several times, and was also observed when the temperature of the water in the aquarium in which the frogs were kept was lowered 10° C. and below. When this was done, all the frogs responded, either by flattening their bodies against the stone floor, or by creeping under the rocks usually kept there. It therefore seems that the frog is stereotropic in temperatures between 10° C. and 4° C."

These experiments of Torelle's, considered with those (*l.c.*, p. 476) on frogs out of water, seem to bear an interesting relation to hibernation. It is probably true that this instinct is not due to a single but to several causes. The increase of stereotropism with a lowering of the temperature is an important physiological change which may be related to the burrowing

response of hibernating frogs. Dickerson (*l.c.*, p. 71) has observed the tendency of young toads, *Bufo americanus* Le Conte, to crawl "under stones and chips, in the cracks of board-walks or under the protecting cover of leaves and grasses." The young toads to which she referred had left the water just recently and were therefore very delicate creatures, and they remained during the daytime in such protected situations as have been mentioned. So that while these responses are probably due in part to contact stimuli, yet other stimuli also such as light and temperature undoubtedly have considerable influence in bringing them about. The burrowing response of young spadefoot toads, *Scaphiopus holbrookii* Harlan, exhibits itself early in the life of the individual (Dickerson, *l.c.*, p. 56), and is in part at least a response to contact. According to Holmes (*l.c.*, p. 351) there is a tendency for frogs and toads to crawl under stones and to place themselves between objects. In such positions they remain quiet. This propensity to move into such situations is more pronounced in the case of toads. He considers such responses to be of a thigmotactic nature, although from his discussion it may be inferred that at times light also plays some rôle.

Considerable care was used in handling the young toads during the experiments with light. They were removed from the aquarium jar and placed in the experimentation trough by hand. In order that such contact should modify the response to light as little as possible, the toads were left undisturbed for approximately fifteen minutes before being subjected to the photic stimuli of the experiment. Should the toads while being transferred from one vessel to another be handled with undue pressure and roughness, they sometimes assume an immobile state. As this response was a somewhat unfamiliar one to the writer a number of observations were recorded concerning it.

Frequently when young specimens of *Bufo americanus* are handled, the contact stimulus causes them to become motionless; they react with the death-feigning response. Certainly they assume an attitude which is comparable to that assumed by many Arthropods when they are said to feign death. The legs are drawn up closely against the body and they assume a more or less rigid condition, the animal remaining motionless. Sometimes a toad lies so absolutely quiet that even the respiratory

movements are unobserved, and the eyes may be closed. The attitude assumed by the death-feigning animal is not always as just described. Instead of the legs being drawn up in close contact with the body they may be somewhat extended. A young toad may be made to feign death by being placed on its back in the hand or on the laboratory table, and held in that position for a few seconds. There is considerable variation among different individuals regarding the length of time of the death-feigning response. Some feign death for a few seconds only, while others retain the death-feigning posture for a minute, and occasionally even for a longer time. When young toads are exposed to the beam of light from the projection lantern during the death-feint, the length of the response seems to be some- what shorter, than when the animals are induced to feign death in weak diffuse daylight. Here again there is much variation, for in some instances it appears to make no difference to the toad as to the intensity of the light to which it is subjected. If the animal is put into the death feint in diffuse daylight and is then exposed to the bright beam of light from the projection lantern, the length of the response is curtailed, in fact the toad at times arouses immediately from the death-feint. A young toad generally arouses from the death-feint rather suddenly. If the animal is on its back, first one leg and then another is extended until the legs are no longer pressed closely against the body. If the eyes are closed while in the death-feint, they are opened sometime during the process of arousing from the re- sponse, while the legs are being extended. Immediately after the eyes have been opened and the legs extended, the toad turns over with the ventral side down. While it is true that the young toad usually arouses from the death-feint rather abruptly, there are individual variations, some animals being more delib- erate in the process than is the case with others. Young toads may be promptly aroused from the death-feint by sudden tact- ual stimuli, as for example, a touch on the body, though this may at times cause a continuance of the response, or by drop- ping them into a jar of water. Dickerson (*l.c.*, pp. 71–72) has observed the death-feigning response in young toads, as indicated by the following quotation:

> "When they are handled they play dead for seconds at a time and finally 'come to life' sticking up their little orange paws in most ridic- ulous fashion before they tumble over and hop away."

Mature specimens of *Bufo americanus* will also feign death. The writer has frequently caused toads to exhibit this response by placing them with the back down and in close contact with some solid surface, meanwhile holding them firmly in that position for approximately thirty seconds more or less. They sometimes respond to stimuli of this nature by feigning death for one or more minutes. Near Ann Arbor, Michigan, the leopard frog, *Rana pipiens* Schreber, is very common. Mature specimens taken in that locality frequently have been made to exhibit the death-feigning response by rough handling and by placing them on their backs on the laboratory table and holding them securely for some time in such a position. Mature toads and frogs exhibit much individual variation in reacting with the death-feigning response. The response is elicited in some animals much more readily than in others. In some instances it seems to be practically impossible to induce the response. The length of the death-feint also varies considerably in different individuals. The death-feigning response is undoubtedly of the same nature as that which Verworn (1898) [3] calls hypnosis. According to this writer specimens of *Rana esculenta* when turned on their backs, become motionless. Sometimes the hind legs are drawn close to the body, and the eyes are closed. While the animals lie in this position, their muscles are in a condition of "tonic contraction." Hypnotized frogs may assume peculiar attitudes, as if in attempting to right themselves the movements were suddenly inhibited. Verworn (1899, pp. 358–359) in discussing the hypnotic state of frogs makes the following statement:

> "The phenomena of prolonged reflex tone after brief stimulation may be seen still more clearly in frogs that have been deprived of their cerebrum. If such a frog sitting quietly in the customary squatting attitude be gently stroked by two fingers along the sides of the spinal column, he raises himself upon his extremities by contracting their muscles, and stands, sometimes more than an hour, in this grotesque position."

According to Verworn (*l.c.*, p. 496) if a frog is seized suddenly and held with a firm grip, and is then placed with its back down the animal remains immobile. A very peculiar contact response on the part of certain toads, *Bombinator igneus* and *Bombinator*

[3] Beiträge zur Physiologie des Centralnervensystems I. Die sogenannte Hypnose der Thieren. Jena, 1898, pp. iv +92. This paper was not accessible, but some discussion of it is given in the section on "Hypnotism," Holmes (1907, pp. 59, 60, 61), and in a review by Gotch (1898).

pachypus, appears to be somewhat akin to the death-feint, or to the hypnotic state already described. The following quotation taken from Gadow (1901, p. 156) gives a good description of the posture assumed by these toads during the response:

> "When these toads are surprised on land, or roughly touched, they assume a most peculiar attitude. * * * The head is partly thrown back, the limbs are turned upwards with their under surfaces outwards, and the whole body is curved up. * * * The creature remains in this strained position until all danger seems passed."

The following interesting description of the death-feigning instinct among toads and frogs is given by Dickerson (*l.c.*, p. 34):

> "Many of the Salientia play dead in response to an unexpected tactual stimulus. The common toad will often hold the legs tight against the body and inhibit all movement—even the breathing vibrations of the throat—when seized by a dog or other enemy. The leopard frog may stretch the legs backwards stiff and straight, fold the arms on the breast, and inhibit the breathing movements. It certainly looks like a dead frog as it lies motionless in one's hand for fully a minute; suddenly, with a lightning movement, it is gone before the hand can be closed over it. The cricket frog plays dead in water. Taking a position with arms and legs rigid and throat collapsed, it floats about helplessly like any stick or leaf."

Dickerson (*l.c.*, 87–88) considers the death-feigning response of the toad to be a protection to the animal. She states that,

> "The toad is fitted for his place in life by what he does, as well as by what he is. Let an enemy seize him roughly, and he is a dead toad. 'Playing dead' saves him many a time. He will lie on his back with scarcely any perceptible motion for minutes at a time. Even the breathing movements seem to be suspended. Suddenly one leg is thrust out, then another, the eyes open wide, and in an instant more, the toad has turned over and is ready for new emergencies. Whether this habit is a protective instinct, or whether the toad really is insensible from fright during the time that it 'plays dead,' the resulting protection is the same, for, as a rule, animals that feed upon living food associate motion with life so firmly that they pay no attention to a motionless creature."

Facts similar to those described by Dickerson have been observed by Holmes (*l.c.*, pp. 59, 60, 61), who considers this immobile condition of the frog to be an hypnotic state. According to this author the position assumed varies at different times. Some individuals are more easily hypnotized than others, and the duration of the hypnotic state also varies in different frogs. Sometimes a frog will remain immobile for hours. A frog may be aroused from its condition of hypnosis by some sudden stimulus, and the awakening often occurs immediately.

Sometimes when removing the young toads from the aquarium jar to the experimentation dish, the writer observed that the

animals respond to contact in another manner than that of the death-feint. The body of the toad is spread out and closely pressed against the bottom of the aquarium, and the ·lungs are filled with air until the animal becomes as wide as it is long. The head is also bent downward and placed on the bottom of the aquarium. As long as the animal retains this position it remains motionless. Reactions similar to these may occur as responses to a moving shadow or object, as for example the writer's hand when it is reached into the aquarium to remove the young toads. So that these are responses to both tactual and visual stimuli. Dickerson (*l.c.*, pp. 33–34, 86) also has drawn attention to this form of response in the toad. According to Holmes (*l.c.*, p. 32),

> "Frogs sometimes swell the body before being seized as if in antici-
> pation of their capture, and they are especially apt to do this after being
> lightly touched. Touch a frog that is resting quietly, and if the creature
> does not hop away, one may see the body puff up; and if the body is
> touched two or three times, the swelling will continue until the lungs
> contain their maximum amount of air. * * * Frogs often avoid
> capture better by remaining perfectly quiet than by attempting to get
> away by jumping. * * * Safety is also sought occasionally by crouch-
> ing close to the ground, and more often by crawling under some object that
> promises to afford shelter."

Another interesting response to contact stimuli is the "singing" or croaking of frogs and toads. The croaking of frogs and toads is readily induced by stroking the body, especially on the back or sides. They also will croak when kept in an aquarium. The contact of one animal against another is often sufficient stimulus to produce this sound. It is not improbable that light as well as contact may play some rôle in connection with the croaking reflex. The writer frequently has observed hundreds of toads in bright patches of moonlight along the shores of ponds and marshes. On such occasions their heads are raised, and the throat-sac is puffed out to a large size, owing to their vigorous "singing." At such times they give little "attention" to the observer, and one may pick up a toad, placing it upon the palm of the hand where it will continue to "sing" with astonishing vigor.

IX. DISCUSSION

It has been pointed out, in the experiments with the projection lantern, that young specimens of *Bufo americanus* orient in such a manner with reference to the light that the head points

away from the source of illumination. After orientation is completed the animals retain the position assumed with reference to the light, the medium longitudinal axis of the body being kept practically parallel with the incoming rays. So far as the writer's observations are concerned, there is no definite evidence that young toads orient to light according to the method of "selection of random movements," as advocated by Holmes (1905) (though the present writer believes that it may function in some modified form), or by that of "trial" so ably propounded by Jennings (1904) and (1906), also discussed by Mast (*l.c.*,), and many other writers. Usually the young toads orient promptly and definitely. If the head is pointing toward the light, they make a turn of 180° so that the anterior end of the body is pointed directly away from the source of illumination. Should the toad be in such a position that the median longitudinal axis of the body lies at right angles to the rays and facing the light, the animal makes a turn of 90°, thus bringing the head into such a position that it points directly away from the source of illumination. There are no preliminary movements, either "trial" or "random" ones, during or immediately preceding the orienting response, so far as the writer observed. But as Mast (*l.c.*, p. 214) has suggested, these facts do not preclude the possibility of preliminary movements when other forms of stimuli impinge upon the toads. After orientation is completed the young toads jump away from the source of illumination along a comparatively straight path, the medium longitudinal axis of the body being parallel with the rays of light. During such motor responses the direction of the rays in the field may be a guiding factor. It is not impossible that they may be both a guiding and a correcting factor, if we should apply the theory advocated by Holmes (*l.c.*, pp. 108–109). While there is little evidence of such responses on the part of young toads, nevertheless the applicability of Holmes's modified "trial and error method" with reference to the responses of animals which orient themselves "according to the usual scheme" is worthy of careful consideration. The present writer believes that it is absolutely futile to attempt to explain the responses of all animals by any one theory, or from any one point of view.

Such a response on the part of young toads as has been described by the writer is a tropic response in so far as it fits

the definition of Jennings (1909, p. 307), however, the writer does not wish to be understood as believing that internal factors, changes in bodily states, play no rôle in the orientation of young toads to light. This matter was not discussed in connection with the responses to intense artificial light, largely because the wr.ter was attempting to record the responses as they occurred in the majority of cases. There are occasional examples when it is observed that one toad orients to the light much more slowly and hesitatingly than another. Some toads jump away from the light more rapidly than others and along a straighter path. There also is found to be variations in such responses on the part of the same animal on different occasions. These facts seem to indicate modifications in the bodily conditions of the animals concerned, especially when it is remembered that both the environment and the kind of stimuli remain unchanged. Loeb (*l.c.*, p. 24) and (1912, p. 47) early recognized the importance of differences in the physiological conditions of animals as modifying factors in animal responses. This subject has been discussed by the present writer (1912, pp. 281–283). It is not improbable, in the writer's experiments with young toads, that before orientation the animals are, as it were, in a condition of unstable equilibrium with reference to the light, and that the orienting response is one of adjustment; and further, after orientation is completed the toads are then in a condition of relative stability toward the light, so far as orientation is concerned, and they exhibit further response by jumping away from the source of illumination. With reference to orientation in general, may it not be a fact that previous to the orienting response the bodily state of the animal differs from its condition after orientation is complete?

The responses of young toads to the light from the projection lantern seem to indicate that the unequal light intensity on the two sides of the body is a factor in inducing the animals to orient so promptly and definitely. According to Holmes (1907, p. 346), frogs orient with respect to light in general in much the same manner. Pearse (*l.c.*, pp. 172–205) apparently takes a similar point of view with reference to the orientation of specimens (some of them immature) of *Bufo americanus* and *Bufo fowleri* to light of 220 ca.m. intensity (see particularly *l.c.*, pp. 204–205). The orientation of specimens of *B. ameri-*

canus (some of them immature), as described by Mast (*l.c.*, pp. 214–215, 219–220) appears to occur much in the same way as observed by the writer in young toads. The intensities of the lights employed by Mast in his experiments were 12.5 and 25 ca.m. It is probable, during the orienting response of young toads, that the light acts in some such manner as described by Loeb (1905, p. 32), and to which Mast (*l.c.*, p. 223) practically assents. Even so, though the light should act "at a constant intensity," such a fact does not necessarily preclude the influence of the differences in intensity on the two sides of the animal's body, during orientation.

In regard to the effect of light intensity upon the orientation of young toads, mention should be made of Mast's (*l.c.*, pp. 219–220) extremely interesting experiments with specimens of *Bufo americanus*, some being immature. Two lights of different intensities were employed, one being 12.5 ca.m. and the other 25 ca.m., and the source of illumination was two Nernst glowers, the two beams of light crossing at right angles. When a toad was placed, with one side turned toward the glower, in the beam of light of lesser intensity, it oriented directly and accurately, and then jumped toward the source of illumination. However, when the animal reached the intersecting beam from the light of greater intensity, instead of orienting toward this light, it continued to jump toward the weaker light. Altogether 42 trials were made, 36 of these being as described. In 6 cases only did the toad turn toward the stronger light when it reached the point of intersection of the two beams, and these six trials were all with the same individual. Seven toads only were used in the experiments. It would seem in a series of experiments exhibiting results of this nature that the effect of light intensity was modified as an orienting factor, or why did not the animals orient toward the light of stronger intensity. The present writer offers two suggestions which may prove to be partially, if not fully explanatory of this. First, the eyes are strongly stimulated by the light from in front, and the response to such stimulation in itself may result in producing an inhibitory effect upon the toad in so far as its response to the stimuli from the intersecting light is concerned. While it is true that in toads both skin and eyes are photoreceptors as Pearse (*l.c.*) has proved, it is evident that the cross rays from the stronger light

would reach one eye only with full effectiveness. Second, if animals with image-forming eyes go toward a source of light, because they perceive the light itself and follow it "much as an animal pursues any other object of interest" as indicated by Graber (*l.c.*, p. 248), Torelle (*l.c.*, p. 471), Holmes (1905a, pp. 341, 344–345) and (1908, p. 496), and Mast (*l.c.*, pp. 219, 223), then such behavior may present a partial explanation as to the reason why the toads used in Mast's experiments did not go toward the stronger light, for the "attention" of the animals may have been so fully occupied with the light in front of them that they did not turn into the intersecting beam, and jump toward the source of the stronger light. Further, it must be recalled, as Mast (*l.c.*, p. 223) himself has suggested, that the direction of the rays in the field may be a guidance to the toads, especially if they go toward an object because they see it. Then, the after effects of the directive weaker light may have been sufficient to keep the toads moving along the path already taken, even when they reached the strong intersecting beam of light. In so far as this work of Mast's applies to the writer's experiments with young toads, certain facts should be kept clearly in mind regarding the latter's experiments, that the animals employed were extremely immature, that light approximating 10,000 ca.m. intensity was used, and that the toads reacted negatively to the photic stimuli. From what is known of the habits of toads, it was to be expected that the animals would respond negatively to the strong stimuli from the projection lantern. Toads are very largely nocturnal animals, and are more commonly seen about twilight when they leave their places of "concealment," which they have occupied during the daytime.

The young toads respond positively to all the lesser light intensities of white light. In these experiments it seems as if the difference in the intensity of the stimuli on the two sides of the body was an important factor in orientation. This subject has been discussed in connection with the responses to the light from the projection lantern, and therefore will not be dwelt upon here. In jumping toward the light it is hardly probable that the rays *per se* in the field are a very important element in guiding the toads, for it has been stated that there must be many cross lights in the field of experimentation. Of course there is a certain part of Holmes's theory (1905, pp. 108–

109) that might apply here as a partial explanation, for a portion of the rays are parallel with each other and with the median longitudinal axes of the bodies of the toads. In the experiments in the dark room the principal object in the toad's field of vision is the light, and it is probable that the animals jump toward it because they see it, an idea that has been mentioned before. The light also may act continuously as Mast (*l.c.*) has suggested, and somewhat as Loeb (1890, p. 90) stated more than twenty years ago with reference to frogs when diffuse daylight was used as a stimulus. The following quotation gives Loeb's point of view:

> "Dass auch beim Frosch das Licht als konstante Reizursache wirkt, geht daraus hervor, dass die Thiere dauernd an dem der Lichtquelle entgegengesetzten Ende des Kastens sitzen bleiben."

In experiments with weak diffuse daylight, orientation is not a prominent feature in behavior, but there is some evidence of a tendency for the toads to gather toward the source of illumination.

Many of the responses of young toads to contact stimuli are probably adaptive ones, such as creeping under and between objects. Even so peculiar a response as that of the death-feint may be of such a nature, as the observations of some writers seem to indicate. It is true that in the case of some of the Arthropods, it is rather more difficult to see how the death-feigning response serves any adaptive purpose. The act of crouching against the ground and of inflating the lungs with air may be another example of a protective device. It would be of considerable scientific interest, for some investigator to make a long and varied series of observations with reference to the contact responses of young toads, and see in how many instances such responses were adaptive in function.

X. SUMMARY

Specimens of *Bufo americanus* Le Conte, approximately 14 mm. in length were collected near Ann Arbor, Michigan. They respond negatively to the light from a projection lantern, with an approximate illumination of 10,000 ca.m. within the field of experimentation. The animals jump away from the light toward the opposite end of the dish. If they are left in that

situation for some time, some of them climb up the perpendic-
ular glass wall at the end of the vessel. This places them out
of the most intense glare of the light. The young toads orient
promptly and definitely, by turning away from the source of
illumination and so place themselves that the longitudinal
axes of their bodies lie parallel with the incoming rays. This
position in relation to the rays of light is maintained while
traveling from one end of the dish to the other, and the pauses
between the jumps are brief, so that the animals move with a
fair degree of speed. The responses in water are similar to those
already described, the toads swimming away from the light.

The young toads respond positively to the light from a 16
c.p. incandescent light, with an illumination approximately of
44 ca.m. They also respond in a similar manner to strong
diffuse daylight, to weak diffuse daylight, and to sunlight. Except
in the case of diffuse daylight, the animals jump toward the
source of illumination in a comparatively straight path. It
cannot be said that the median longitudinal axes of the bodies of
the toads are parallel with all the incoming rays, because many
of the rays enter the experimentation dish at various angles
and there must be cross lights within the field of experimenta-
tion. While the animals jump toward the light with consider-
able promptness, their motor responses are perhaps not so
quick as in the experiments with the projection lantern. At
times it seems as if the toads do not travel in quite so straight
a path as is the case when the intense artificial light is used as
a source of stimulation. The toads orient fairly definitely and
accurately, but not so promptly as when the projection lantern
is employed. At times, when responding to sunlight, the animals
come to rest in diffuse daylight, if it is nearby. Neither the
movement toward the light nor the orientation is so definite as
in the case of the stronger intensities.

. It is not improbable that both light intensity and ray direc-
tion in the field are factors in these photic responses. During
orientation light intensity may play the more important rôle,
while the rays in the field may act as a guiding factor after
orientation is complete, though this does not necessarily do
away with the effect of intensity. In the positive responses
vision is an element not to be ignored, and it is probable that

the light acts continuously. Further, it is not impossible that a modified form of "trial and error" may function as the animals travel toward or away from the source of illumination. In the experiments with weak diffuse daylight, ray direction in the field probably exerts comparatively little influence upon young toads.

Young toads react to light passed through red and blue solutions by giving motor responses. When red light is employed singly, it is noticed that the stimuli are not very effective. There is a tendency for the animals to act negatively, both by turning and jumping away from the light. The responses are less definite than when either white or blue light is used. When blue light is employed the toads both turn and jump toward the light, and they do so with more promptness, than is the case when red light is used. When red and blue lights are used at the same time, more animals jump toward the blue light than they do toward the red light. Some toads jump toward the red light, and a few individuals appear to be indifferent.

Young toads subjected to light react to contact stimuli by giving the motor response. If a stationary individual is stimulated by another animal jumping against it, the former responds either by turning or by jumping away. Frequently after such a motor response, the animal follows it up by reacting to the light. In the experiments with the lesser light intensities, the young toads may respond to contact by several of them gathering in the angles formed by the bottom and sides of the experimentation dish. They remain in such situations with their bodies in close contact.

Young toads frequently react with the death-feigning response when handled with undue pressure and roughness. During such response they remain immobile, with their legs drawn up against the body. A toad may be caused to respond in this manner by placing the animal on its back and holding it in that posture for a few seconds. The length of the death-feint varies in different individuals. If a toad has been made to feign death in diffuse daylight, the response may be curtailed by suddenly flashing a beam of light from the projection lantern upon the animal. Young toads usually arouse from the death-feint abruptly. A sudden tactual stimulus will effect this. The death-feigning response may probably result in producing

a bodily condition in young toads not far removed from that of hypnosis described by Verworn in other animals.

Young toads will also respond to contact in another manner. Sometimes when touched the body is pressed closely against the ground, and the lungs are inflated with air, the head also being bent downward. While in this position an animal remains motionless. It is likely that many of these responses to contact on the part of young toads are adaptive in function.

XI. BIBLIOGRAPHY

COLE, L. J.   An Experimental Study of the Image-Forming Powers of Various
    1907.   Types of Eyes. Proc. Amer. Acad. Arts and Sci., Vol. XLII, No.
                16, pp. 335–417.
DICKERSON, M. C. The Frog Book. New York, xvii + 253 pp.
    1906.
GADOW, H.   Amphibia and Reptiles. Cambridge Natural History, London and
    1901.   New York, Vol. VIII, xiii + 668 pp.
GOTCH, F. The Hypnotising of Animals. Nat. Sci., Vol. XIII, No. 82, pp. 417–
    1898.   419. (Review of Beiträge zur Physiologie des Centralnervensys-
                tems I. Die sogenannte Hypnose der Thieren. By Max Verworn.
                Jena, G. Fischer. 1898. Pp. iv + 92.)
GARBER, V. Grundlinien zur Erforschung des Helligkeits- und Farbensinnes der
    1884.   Tiere. Prag und Leipzig, viii + 322 pp.
HOLMES, S. J. The Selection of Random Movements as a Factor in Phototaxis.
    1905.   Jour. Comp. Neurol. and Psychol., Vol. XV, No. 2, pp. 98–112.
    1905a. The Reactions of Ranatra to Light. Ibid., Vol. XV, No. 4, pp. 305–
                349.
    1907. The Biology of the Frog. 2d ed. New York and London, ix + 370 pp.
    1908. Phototaxis in Fiddler Crabs and its Relation to Theories of Orienta-
                tation. Jour. Comp. Neurol. and Psychol., Vol. XVIII, No. 5,
                pp. 493–497.
JENNINGS, H. S. Contributions to the Study of the Behavior of Lower Organ-
    1904.   isms. Carnegie Inst. of Washington, Pub. No. 16, Washington,
                256 pp.
    1906. Behavior of the Lower Organisms. New York, xiv + 366 pp.
    1909. Tropisms. Rapport au VIme Congrès International de Psychologie,
                Genève, pp. 307–324.
LAURENS, H. The Reactions of Amphibians to Monochromatic Lights of Equal
    1911.   Intensity. Bull. Mus. Comp. Zoöl., Harvard College, Vol. XLIII
                No. 5, pp. 251–302.
LOEB, J, Der Heliotropismus der Thiere seine Uebereinstimmung mit dem
    1890.   Heliotropismus der Pflanzen. Würzburg, 188 pp.
    1905. Studies in General Physiology. Chicago, Part I, XIII + 423 pp.
    1912. Mechanistic Conception of Life. Chicago, 232 pp.
MAST, S. O. Light and the Behavior of Organisms. New York and London, xi +
    1911.   410 pp.
MILLER, N. The American Toad (Bufo Lentiginosus Americanus, Le Conte).
    1909.   Amer. Nat., Vol. XLIII, Nos. 515, 516, pp. 641–745.
NAGEL, W. A. Ueber flüssige Strahlenfilter. Biol. Cent., Bd. XVIII, Nr. 17,
    1898.   pp. 649–655.
PARKER, G. H. The Skin and the Eyes as Receptive Organs in the Reactions
    1903.   of Frogs to Light. Amer. Jour. Physiol., Vol. X, No. 1, pp. 28–36.
PEARSE, A. S. The Reactions of Amphibians to Light. Proc. Amer. Acad. Arts
    1910.   and Sci., Vol. XLV, No. 6, pp. 161–208.

PLATEAU. F.   Recherches expérimentales sur la vision chez les arthrópodes. Quat-
1889.   rième partie. Mém. cour. Acad. roy. Belgique, t. XLIII, 91 pp.
RILEY, C. F. C. Observations on the Ecology of Dragon-Fly Nymphs: Reactions
1912.   to Light and Contact. Ann. Ent. Soc. Amer., Vol. V, No. 3, pp.
            273–292.
TORELLE, E.   The Response of the Frog to Light. Amer. Jour. Physiol., Vol.
1903.   IX, No. 6, pp. 466–488.
VERWORN, M.   General Physiology. Trans. by F. S. Lee. New York and London,
1899.   xvi + 615 pp.

Ecological Laboratory, University of Illinois, January 31, 1913.

THE STIMULATION AND THE INHIBITION OF OVULATION IN BIRDS AND MAMMALS

WALLACE CRAIG

The University of Maine

A previous article (Craig, 1911) by the present writer showed that in six cases female Ring-Doves (*Turtur risorius*) were induced to lay by the courting behavior of male doves though the introduction of sperm was prevented. And in one case a female dove laid her eggs in due time after being stimulated merely by a human being who spoke kind words to her and stroked her head and neck in a friendly way. The opinion was expressed that this last experiment could be repeated if one could get a dove sufficiently tame and willing to show courting behavior toward a human being, as doves sometimes do.

This expectation was fulfilled in the year 1911, with dove No. 41, a young female which had been reared in isolation, which therefore had had no experience with a dove mate, but regarded human beings as her companions. Human beings were kept away from her cage so far as possible until April 25, when the experimenter suddenly began to spend much time near her cage, to put his hand in the cage, and sometimes to preen her head and neck. The dove began next day to respond to the hand with nest-calling behavior (though she was given no nest) and on May 3 she laid her egg. I now find, too, that the same experiment was performed centuries ago by Harvey, on a parrot. "Harvey records that, by stroking the back of a favorite parrot (which he had possessed for years and supposed to be a male), he not only gave the bird gratification,—which was the sole intention of the illustrious physiologist,—but also caused it to reveal its sex by laying an egg." (Robinson, 1892, p. 1295).

It is well known to pigeon breeders that two female pigeons kept together may mate and lay eggs. Some experiments have been made by the writer in mating a female Ring-Dove with another female. In all such cases the two females have gone through a courting performance and in due time both have laid eggs; and after a period of incubation they have repeated the

215

courting performance and the egg-laying. This was observed in the year 1911 in two cases, and in 1912 in twenty-four cases, involving six birds. A very significant detail is, that as the three pairs of females in 1912 were kept in one room, with no other birds in the room, the three pairs showed a marked tendency to keep time with each other in their laying. Each pair could not see the other pairs, but when they heard their excited cooing and kahing and running about, the tardiest pair were thereby stimulated and brought into similar activity.

The mate is not the only environmental factor in determining the time of egg-laying in the dove. As Professor Whitman said to me: "A great many factors enter in. Even if the female has the male, if she has no nest box and no nesting conveniences she may not lay. The egg develops and passes down the oviduct by degrees corresponding to the whole activity of the pair. It takes a week to ten days (in the domestic pigeon). This is true whether the pair are building their first nest or are preparing for a second brood. If, when the female is ready the male is not, she waits for him." In order to prevent birds from laying too late in autumn or too early in spring, Professor Whitman found that it was not always necessary to separate the sexes: he could keep mates together but with no nesting facilities, nothing to "go to work with," and this prevented their breeding. An excellent account of this matter is to be found in a paper by Harper (1904). That the female pigeon will refrain from laying if conditions do not satisfy her, has been so long known to breeders that it is mentioned by Aristotle (1891), who says, "Pigeons are able to retain their eggs even in the act of parturition. If they are disturbed by anything occurring in the neighbourhood of their nest, or a feather be plucked out, or if anything else troubles or disturbs them, they retain the egg they were about to lay." In two cases among my doves this year I observed a bird hold back her egg at the time of parturition, because she was kept away from her nest. However, when the egg is fully developed and ready to lay, the bird's power to retain it is evidently limited. The real control of the production of eggs is earlier, connected with the ovary itself and the process of ovulation.

Professor Whitman had one season a solitary female American robin, which built a nest by herself and laid a set of eggs in it.

This is a familiar occurrence in many species of birds. In such cases it is sometimes assumed simply that the maturing of eggs is the cause of the nest-building. But the reverse is no doubt equally true; the activity of building and the contact with the comfortable nest stimulate the development of eggs. The visceral and the peripheral activities of the bird are in reciprocal relation; each stimulates the other, and they proceed step by step together. It is a case of "circular activity" (Baldwin, 1906). Contact with the nest, under appropriate conditions, exerts a powerful suggestive or an almost hypnotic influence upon the bird, causing in her an emotional attitude which somehow involves the ovaries. This attitude leads her to work further upon the nest. Such work causes the stimulus from the nest to be repeated. Thus the circular activity goes on and on.

In the paper on the influence of the male on ovulation, I said (Craig, 1911, p. 300): "The influence of the male in inducing oviposition is a psychological influence." The reviewer of that paper in the Psychological Bulletin (Washburn, 1912, p. 309) says: "The word 'psychological' is perhaps a little extreme here: the tactile stimuli produced by the male's preening of the head and neck of the female might operate reflexly." No doubt a reflex arc is involved here as in all nervous action; but it is not a simple reflex. It is a reflex which is set working, not by any one sense stimulus, but by the total situation including both the totality of present sense stimuli and also memory factors.

The one condition necessary to induce ovulation is that the female should accept the attentions paid to her and throw herself into the mating and laying attitude.[1] When she does so, her whole organism is affected. Her posture in standing and her carriage in walking are greatly altered. She follows the male to the nest and spends hours in dedicating and building that structure (whereas a solitary female pays no attention to a nest, under normal conditions). Her whole bearing shows intense emotion, not violent, but deep. As the days pass, this manner grows upon her, becoming an extreme attitude at the time of egg-laying.

---

[1] The mating and the laying attitudes may be said to be two attitudes which are subdivisions of one more general. In the ordinary course of the brood cycle, the two are closely united. But I think I have seen each occur quite without the other. In Case 2 (Craig, 1911), for example, there seemed to be no mating attitude whatever, only a laying attitude.

This great transformation is determined by the entire social situation which changes the dove from the status of the un- mated (or it may be from some other stage in the brood cycle) to the status of matehood. No one factor determines it—not the mechanical stimulation of the neck feathers, nor the act of billing (which was one of Harper's suggestions), nor even copulation. As to the preening of the neck feathers: I once tried persistently preening the neck feathers of a dove which refused to accept such action as from a mate: she showed no laying attitude and laid no eggs. A dove which has been ab- ruptly separated from her mate and given a strange male, though that male preens her neck feathers and plays up to her perfectly, may remain quite unstimulated. Conversely, the females which were paired with their own sex, as above men- tioned, preened one another very little as compared with males; yet they accepted each other as mates, and they laid eggs. As to billing: These females mated with females again illus- trate, for they billed but little and imperfectly, in some cases not billing at all. And in the case of the birds induced to lay by hand, there was of course complete absence of billing. As to copulation: That this is not a necessary factor is proved by the cases in which the female was induced to lay by preening the feathers of the head and neck. Bartelmez (1912, p. 290) mentions that a female may lay even when the male stimulat- ing her is in another cage. Conversely, there are cases in which a pair copulate regularly, yet the female does not lay. And in some such cases the cause seems unquestionably to be that the female is dissatisfied, as with her nest or other circumstances, hence does not get into the laying attitude above described, and consequently does not ovulate. I think that in some, though not in all cases, one could prevent ovulation in a mated female by persistently following her and turning her out of any corner where she began to settle in the laying attitude.

Data which will be given at length in other articles, show that there is a difference in this respect between young doves which have never mated and old doves which have been breed- ers for years. The inexperienced are more ready to enter into abnormal matings,—as, with their own sex, or with alien spe- cies, or with the hand,—or to lay without a nest. They lay eggs in conditions under which an old experienced dove would

refuse to do so. Indeed, the assumption of the egg-laying attitude is, to a limited degree, a voluntary activity (if the word voluntary may be applied to animal activities), for it depends upon the dove's disposition, her whole past history, and her whole attitude toward the present situation.

Just as certain environmental conditions stimulate egg-laying, so there are certain environmental conditions which inhibit it. Some of the facts already given illustrate such inhibition. A clear case of it is seen in species of birds of which the female tends to lay eggs continuously until they reach a certain number, the sight of which (or the touch?) inhibits further laying. Egg collectors have often caused such a bird to lay an abnormally large number of eggs, by leaving only one "nest egg" in the nest, removing every additional egg as soon as it appears. Perhaps the most remarkable instance recorded is that of a flicker (*Colaptus auratus*) experimented on by Mr. Charles L. Phillips, of Taunton, Mass. "On May 6, 1883, he found a cavity in a large willow tree containing two eggs; he took one, leaving the other as a 'nest egg,' and continued to do so day after day until the female flicker had laid seventy-one eggs in seventy-three days." (Davie, 1898.)

Columbidae do not prolong their laying in this manner. In them, the number of eggs in a set is predetermined in the ovary, and is never more than two. But it is clear that all through the incubation period the presence of eggs in the nest prevents the ripening of the new set of ova, which will ripen as soon as the bird reassumes the laying attitude. That the sight of eggs in the nest can inhibit the assumption of the mating attitude, is shown by the following scene, which is familiar to every keeper of pigeons or doves: The hen dove is sitting on her eggs; her mate comes to her with bowing coo and other signs of intense excitement; she is gradually aroused, rises, shows a mating attitude, and starts to leave the nest; then she catches sight of the eggs, and as she looks at them her attitude changes toward that of brooding; she stands hesitant for several seconds, drawn one way by the stimulus from the mate and the other way by the stimulus from the eggs; gradually the brooding attitude becomes stronger, the mating attitude disappears, she goes back and settles on the eggs. But if now the eggs be removed from the nest, the hen dove loses her brooding attitude, and it

may be, as Professor Whitman observed, only a half hour until the birds are at work preparing for another laying.

When wild birds (and other animals) kept in captivity refuse to breed, the trouble in many cases is surely psychological. It is not that the birds are in poor health, or have improper food, etc. It is that the conditions fail to stimulate or even positively inhibit the arousal of their breeding instincts and of the associations formed during their wild breeding experience.

Between the different species and different orders of birds there are great differences in the relation of ovulation to environmental conditions. The stimulation of ovulation by the social activity of the male occurs no doubt in all the Columbidae and probably in a great many other monogamous birds. The domestic fowl and perhaps all the Phasianidae (Craig, 1911; Harper, 1904, p. 353) present an extreme contrast to the pigeons, in that their ovulation is highly independent of mating. Parasitic layers such as the European Cuckoo and the North American Cowbird (*Molothrus ater* Bodd) are probably descended from forms whose ovulation resembles that of the pigeon, but have evolved to a state in which ovulation is more independent of environment, at least not depending upon any stimulus of the bird's own nesting activity. This is in agreement with the conclusion of Herrick (1910, p. 232) that the habit of parasitic laying is connected with a disturbance of the "attunement of egg-laying to nest-building."

Harper (1904, p. 352) hinted that what we have said of pigeons does not apply at all to the Mammalia, that in the latter ovulation is "exclusively a female function." But this is an error. It has been shown for many Mammals (Thomson, 1839, p. 44; Marshall, 1910, pp. 134–139; Longley, 1910) that ovulation is favored by or may even depend upon union with a male. And there is reason to believe that what is true of pigeons is true also of these mammals: that in so far as ovulation is dependent upon environment, it is dependent, not upon any one afferent stimulus, but upon the entire situation—involving the female's inborn disposition, her whole past history (see pp. 215–218) and all factors in the present environment which affect the social, emotional situation.

REFERENCES

ARISTOTLE.   History of Animals.   Trans. by Richard Cresswell.   London.   See
1891.   end of Chapter II, Book VI, p. 141.

BALDWIN, J. M.   Mental Development in the Child and the Race: Methods and
1906.   Processes.   3rd ed.   New York.

BARTELMEZ, G. W.   The Bilaterality of the Pigeon's Egg.   Jour. Morph., Vol.
1912.   23.

CRAIG, W.   Oviposition Induced by the Male in Pigeons.   Jour. Morph., Vol. 22.
1911.

DAVIE, OLIVER.   Nests and Eggs of North American Birds.   5th ed.   Columbus.
1898.

HARPER, E. H.   The Fertilization and Early Development of the Pigeon's Egg.
1904.   Am. Jour. Anat., Vol. 3.

HERRICK, F. H.   Life and Behavior of the Cuckoo.   Jour. Exp. Zool., Vol. 9.
1910.

LONGLEY, W. H.   Factors which Influence the Maturation of the Egg and Ovula-
1910.   tion in the Domestic Cat.   Science, N. S., Vol. 31, pp. 465–466.

MARSHALL, F. H. A.   The Physiology of Reproduction.   London.
1910.

ROBINSON, LOUIS.   Art. "Ticklishness."   Tuke's Dictionary of Psychological
1892.   Medicine.   2 vols.   London.

THOMSON, ALLEN.   Art. "Generation."   Vol. 2 of the Encyclopedia of Anatomy
1839.   and Physiology, ed. by Robert B. Todd.

WASHBURN, M. F.   Recent Literature on the Behavior of Vertebrates.   Psychol.
1912.   Bull., Vol. 9.

SOME REFLECTIONS ON THE ORIGIN AND SIGNIFICANCE OF THE CEREBRAL CORTEX

C. JUDSON HERRICK

University of Chicago

Four figures

What are the elements of consciousness? Psychologists used to talk about simple sensations, elementary feelings and pure volition, but most of us have difficulty in finding these things introspectively. Our sensations and volitions are inextricably interwoven with each other and with ideas of various grades of complexity. The child is born with definite physiological capacities for reflex response to stimuli and with certain impulses and instinctive tendencies, none of which necessarily involve any conscious element. On this foundation he builds up by slow increment his mental life.

The intellectual superstructure is not built up out of simple sensations, which are first compounded into perceptions and then disembodied as ideas; quite the contrary, the child's first experiences are with completed physiological circuits, kicking, sucking and the like, and these are soon elaborated in accordance with his innate impulsive and instinctive endowment into complex behavior types, which are rapidly modified by experience. The mental elements, from the genetic point of view, are to be sought in these behavior complexes, rather than in any abstractions derived by a process of logical analysis from philosophical postulates or highly sophisticated adult introspection.

What these first mental elements may be in the very young child it is impossible for a man (even though he be a psychologist) to determine by any simple method; but many of our adult mental processes arise apparently immediately from a conflict of two or more instincts or automatisms no one of which would necessarily by itself have any mental content. And these mental processes in turn resolve themselves into action and run down into automatism again.

The plain man who is not versed in the subtleties of philosophical dialectic or introspective analysis is apt to conclude that

the units which we recognize in consciousness in the simplest mental processes which we can observe are not simple elements at all, but complexes of sensation, feeling, impulse, or what-not, whose character is in some measure predetermined in each case by the organization of the physiological circuit with which it is genetically related. Without attempting here a justification of this conclusion on psychological grounds, let us inquire how it accords with what we know of cerebral structure.

There are no afferent tracts leading to the cerebral cortex directly from any peripheral sense organ or from any center within the brain which is "pure," i.e., devoted to a single sensory function. In other words, no simple sensory impulses ordinarily reach the cortex, but only nervous impulses arising from lower correlation centers, where complex reflex combinations of various sensory systems are possible. The optic impulses reach the cortex most nearly pure, i.e., with less subcortical associational relation with other sensory systems (it is no accident that the visual sense plays a dominant rôle in human cortical function);[1] but even here the optic centers in the thalamus from which optic projection fibers arise are intimately related with acoustic, tactile and other important sensory centers. And in the case of all of the other sensory systems, the projection fibers which enter the cortex come from centers which are separated from their respective sense organs by two or more association centers of a high order of complexity. Each of these subcortical associational centers may be dominated physiologically by a single sensory system, but it is structurally adapted for bring-

---

[1] The optic apparatus is peculiar in that the cortical optic path, instead of first passing through the lower reflex centers (optic tectum) on its way to the thalamus, as in the case of the other sensory systems, is short-circuited in the pulvinar and lateral geniculate body before the mesencephalic centers for the simpler optic reflexes are reached. Sherrington's researches on sensual fusion (Integrative Action of the Nervous System, chap. 10) have shown that the sensory stimuli received from each eye are independently elaborated subcortically, but that the fusion of the uniocular sensation complexes into a single mental image is cortical. "The binocular combination must be a synthesis of a left eye with a right eye *sensation.*" "The singleness is therefore the product of a synthesis that works with already elaborated sensations contemporaneously proceeding" (p. 383). The separateness of the cerebral processes for the two eyes is probably correlated with the necessity for accurate spatial localization in the field of vision. Similarly, some elements of cutaneous sensibility, where accurate spatial localization in consciousness is also highly developed, reach their thalamic centers very directly through the medial lemniscus (Head and Holmes, Brain, vol. 34, 1911), while others pursue a more indirect route through the lateral lemniscus, the latter type of connection being the more primitive.

ing that system into relation with several others, so that the nervous discharge which emanates from it may be the efferent link in a very complex reflex arc. This efferent discharge may descend to the appropriate motor center, or it may ascend to enter a still higher association center, all of whose afferent tracts come from similar lower centers and therefore carry nervous impulses which represent a sort of physiological resultant of the functional factors there interacting.

A few selected illustrations of the various types of correlation centers may clarify these relations. Fig. 1 illustrates the simplest reflex arc. An auditory impulse coming to the brain terminates in a primary acoustic center in the superior olive,
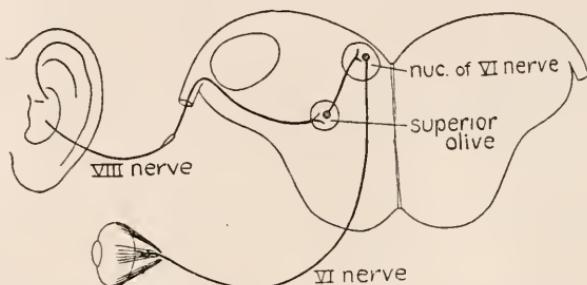
FIGURE 1.—Diagram of a simple auditory reflex. Upon stimulation of the endings of the VIII nerve in the ear by sound waves, a nervous impulse may pass to the superior olive, whence it is carried by an intercalary neurone of the second order to the nucleus of the VI nerve. The fibres of this nerve end on the external rectus muscle of the eyeball.

where it is taken up by an intercalary neurone and transmitted to the nucleus of the VI nerve. The result is a contraction of the external rectus muscle of the eyeball, turning the eye toward the side from which the auditory stimulus was received. (There is another path leading to the nucleus of the III nerve for the innervation of the internal rectus muscle of the other eye, thus providing for conjugate movements of the two eyes—but that is another story.) This reflex arc operates *per se* in a purely mechanical fashion to produce a determinate invariable type of response.

Other fibers arising in the primary acoustic center may ascend to the roof of the midbrain (corpora quadrigemina), where they are brought into relation with fibers belonging to other functional systems. In the lower amphibian brains (e.g., the com-

mon mud-puppy, Necturus) this associational mechanism is the simplest possible (Fig. 2). Here the upper part of the midbrain roof receives optic fibers from the optic tracts, while the lower part receives lemniscus fibers from the primary acoustic and tactile centers. A single neurone of the midbrain may send one dendrite upward to receive optic stimuli and another dendrite downward to receive acoustic or tactile stimuli (or both of these). If the animal receives visual and auditory stimuli simultaneously, the intercalary neurone of the midbrain may be excited by both sets of stimuli. Its discharge through the
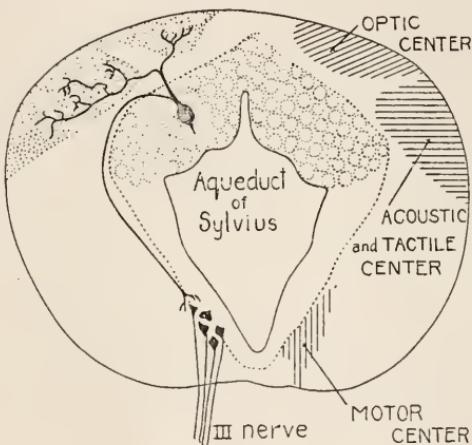
FIGURE 2. Diagram of a cross-section through the midbrain of Necturus, illustrating a single association neurone of the midbrain roof. One dendrite spreads out in the optic center among terminals of the optic tracts; another dendrite similarly spreads out in the acoustic and tactile center. The axon descends to connect with the motor neurones of the third nerve.

axon to the motor organs of response (say to the eye-muscles by way of the third nerve, as in Fig. 2) will be the physiological resultant of both sets of excitations. If they reinforce each other, the discharge will be stronger and more rapid; if, on the other hand, they tend to produce antagonistic responses, there will be an inhibition of the response or a delay until one or the other stimulus obtains the mastery.

In the human brain the corresponding structures are similar in functional type, but much more complex, with many systems of intercalary neurones between the different functional centers. The midbrain roof (corpora quadrigemina) is differentiated into

a superior colliculus for optic impressions and an inferior colliculus for auditory impressions, with a complicated system of associational neurons putting these secondary centers into physiological relation. But the final motor discharge in each case may be the result of the reaction of the whole apparatus and not of either the optic or the auditory center alone.

A further complication arises from the fact that the efferent tract is not simple, as diagrammed in Fig. 2; but it divides into a descending and an ascending path. The former connects directly with motor centers, including the oculo-motor, bulbar and spinal motor nuclei, while the latter enters the thalamus, where associations of a still higher order are effected (Fig. 3).
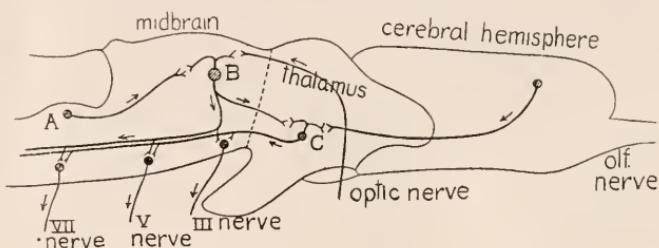
FIGURE 3. Diagram of some conduction paths in the brain of Necturus, seen in longitudinal section. From the medulla oblongata an acoustic impulse may be carried forward through the neurone *A* to the midbrain, whose neurones, *B*. are of the type shown in Fig. 2, receiving both acoustic and optic impulses. This neurone *B* may discharge downward to the motor nuclei of the III, V, VII, etc., nerves, or it may discharge upward to a neurone of the thalamus, *C*, which also receives descending impulses from the cerebral hemisphere.

Here is introduced a physiological choice or dilemma; the response is not a simple mechanical resultant of the interacting stimuli, but its character may be influenced by variable physiological states. The determinate type of action is replaced by a relatively indeterminate or labile type. In the thalamus the nervous impulse is again subjected to modification under the influence of a still greater variety of afferent impulses, for these centers receive all sensory types found in the midbrain, and in addition important descending tracts from the cerebral hemispheres—in lower vertebrates the latter are chiefly olfactory. In fishes and amphibians few optic fibers enter the thalamus directly, but most of these pass by to end in the midbrain.

The fibers which enter the thalamus in general come from other association centers and therefore may carry impulses which have been already elaborated into rather complex systems of

reflexes, rather than simple sensory elements. In the thalamic centers these reflex systems in turn become the units involved in a further process of coördination, the resultant responses being still further removed from the rigidly determinate type of response characteristic of the simple reflex arc. The efferent neurons of the thalamus, like those of the midbrain, discharge into the cerebral peduncles and lower motor centers, but the reflex and instinctive responses thus brought to pass are of a more complex sort than those of the primary and secondary correlation centers of the medulla oblongata and midbrain, and are far more easily modifiable by experience and by variable physiological states.

The thalamus of lower vertebrates (say all species below the frog) is probably the organ of the highest associations of which these animals are capable. These are mostly on the reflex and instinctive plane, though of course a limited psychic factor cannot be excluded. The cerebral hemisphere of fishes is dominated by the olfactory system, as the midbrain is by the optic system, and, so far as may be inferred from the anatomical evidence, is by no means so efficient an associational mechanism as the thalamus. There is nothing in these animals which can be compared, when physiologically considered, with the mammalian cerebral cortex, though the primordia from which that cortex has been derived in higher animals can be readily identified in them. It is indeed clearly established that the hippocampal formation (archipallium) has been differentiated from the dorso-medial segment of the wall of the primitive cerebral hemisphere, while the rest of the cortex (neopallium) was elaborated from materials found in the lateral wall of the hemisphere, the somatic area of Johnston. But in fishes and the lower amphibians there is nothing here which conforms to our ideas of cerebral certex, either structurally or functionally considered.

It is a far cry from an identification of the topographic sources of the structural material from which the cerebral cortex has been gradually elaborated to an adequate understanding of the functional factors which have effected that differentiation. As well might one say that the discovery of the quarries from which the materials for the Parthenon were dug would give an adequate explanation of that architectural masterpiece.

Starting from the very primitive "somatic area" of fishes, we can trace in amphibians, reptiles, birds and mammals the gradual differentiation of the non-olfactory parts of the cerebral hemispheres. In the initial stages of its evolution this structure is organized much like the thalamus. It receives no afferent fibers which come directly from any simple primary sensory center, but only fibers from association centers of the second or third order, which are themselves capable of elaborating complicated reflex responses.

The thalamus, as we have seen, has its own intrinsic system of association centers, which discharge downward into the cerebral peduncles, and this is the primary reflex apparatus of this part of the brain. The thalamo-cortical connections arose to prominence later in the evolutionary history, though feeble rudiments of these are present in lower brains. Parallel with the enlargement of these cortical connections a special part of the thalamus was set apart for them and from the Amphibia upward in the animal scale this dorsal part of the thalamus assumed increasingly greater importance. This part is termed by Edinger the neothalamus and makes up by far the larger part of the thalamus in the human and all other mammalian brains. It occupies the dorsal part of the thalamus proper and comprises most of the great thalamic nuclei (anterior, lateral and ventral nuclei pulvinar and lateral and medial geniculate bodies). The primitive intrinsic reflex thalamic apparatus in man is a relatively unimportant area of medial grey matter and the subthalamic region (corpus Luysii, lattice nucleus, etc., not to be confused with the hypothalamus which lies farther down in the tuber cinereum and mammillary bodies).

The neothalamus, accordingly, serves as a sort of vestibule to the cortex, every afferent impulse from the sensory centers (except the olfactory system) being here interrupted by a synapse and opportunity offered for a wide range of subcortical associations. The olfactory cortex (hippocampal formation) has a similar relation to subcortical correlation centers in the olfactory area in the anterior perforated space, septum, etc.

From these anatomical considerations it follows that no simple sensory impulse can, under ordinary circumstances, reach the cerebral cortex without first being influenced by subcortical association centers, within which complex reflex combinations

may be effected and various automatisms set off in accordance with their preformed structure. These subcortical systems are to some extent modifiable by racial and individual experience, but their reactions are chiefly of the determinate or stereotyped character, with a relatively limited range of possible reaction types for any given stimulus complex.

It is shown by the lower vertebrates which lack the cerebral cortex that these subcortical mechanisms are adequate for all of the ordinary simple processes of life, including some degree of associative memory. But here, when emergencies arise which involve situations too complex to be resolved by these mechanisms, the animal will pay the inevitable penalty of failure—perhaps the loss of his dinner, or even of his life.

In the higher mammals with well developed cortex the automatisms and simple associations are likewise performed in the main by the subcortical apparatus, but the inadequacy of this apparatus in any particular situation presents, not the certainty of failure, but rather a dilemma. The rapid preformed automatisms fail to give relief, or perhaps the situation presents so many complex sensory excitations as to cause mutual interference and inhibition of all reaction. There is a stasis in the subcortical centers. Meanwhile the higher neural resistance of the cortical pathways has been overcome by summation of stimuli and the cortex is excited to function. Here is a mechanism adapted, not for a limited number of predetermined and immediate responses, but for a much greater range of combination of the afferent impressions with each other and with memory vestiges of previous reactions and a much larger range of possible modes of response to any given set of afferent impressions. By a process of trial and error, perhaps, the elements necessary to effect the adaptive response may be assembled and the problem solved.

It is evident here that the physiological factors in the dilemma or problem as this is presented to the cortex are by no means simple sensory impressions, but definitely organized systems of neural discharge, each of which is a physiological resultant of the reflexes, automatisms, impulses and inhibitions characteristic of its appropriate subcortical centers. The precise form which these subcortical combinations will assume in response to any particular excitation is in large measure determined by the

structural connections of these centers *inter se*. And the pattern of these connections is tolerably uniform for all members of any animal race or species. This implies that it is hereditary and innate. This is the underlying basis of instinct.

The connections between the cortical centers, on the other hand, are much less definitely laid down in the hereditary pattern. The details of the definitive association pattern of any individual are to a greater degree fixed by his particular experience. This is the basis of docility and the individually modifiable or intelligent types of behavior. The typical cortical activities, even when physiologically considered, are far removed indeed from those of the brain stem.

It should be emphasized, however, that the differences between the cortex and the lower centers of the brain stem, so far as these can be deduced from a study of structure and from physiological experiment, are relative and not absolute. Indeed the general pattern of the regional localization of the cortex itself is innate and in adult life the cortex has acquired many more characteristics similar to those of the brain stem, with its own systems of acquired automatisms and habitually fixed types of response. The larger association centers retain their plasticity longest, but ultimately these also cease to exhibit new types of coördination and this marks the onset of senility.

The cerebral cortex, then, is not to be likened to the seat of an absolute monarch who receives his messages from outlying parts of his empire in the form of simple sensations and executes his will directly upon his subjects, the bodily organs; but rather to an upper house of parliament with limited powers of initiating legislation *de novo*, but with remarkably extensive capacity for the revision and amplification or veto of such bills as are sent up to it from the lower house and with a very efficient direct control over the entire administrative machinery of the government.

Dewey's stimulating analysis[2] of the reflex arc concept, or as he prefers to say, the organic circuit concept, implies that the synthesis of the elements of a complex chain reflex into an organic unity is the essential prerequisite of that apperceptive

---

[2] The Reflex Arc Concept in Psychology. *Psych. Rev.*, vol. 3, p. 357, 1893. See also Dewey's later statement in *Jour Philos., Psych. and Sci. Methods*, vol. 9, Nov., 1912, pp. 664-668, especially the footnote on p. 667.

process which will make the total experience of value for future discriminative responses — for learning by experience. This, which is true in the individual learning process, is also true phylogenetically. The coördination centers (and their capacity for the preservation of vestiges of past reactions) are the organic mechanism for this synthesis. They make it possible that a new stimulus may be reacted to, not as a detached element, but as a component of a complex series of past and present adjustments, to which it is assimilated in the association centers—apperception. This assimilation or apperceptive process is an integral part of the receptor process in the higher centers, giving the quale to the idea of the exciting object. Cotemporaneously with this stimulus-apperception process we have an apperception-response-activity giving the object-or purpose-idea, so that the entire reaction is to be regarded as stimulus-apperception-response, as a functional unity rather than as a sequence: stimulus > apperception > response.

Dewey's organic circuit concept is elaborated in terms of psychology. Let us see how it may be applied to biological behavior.

The simple reflex is commonly regarded as a causal sequence: given the gun (a physiologically adaptive structure), load the gun (the constructive metabolic process), aim, pull the trigger (application of the stimulus), discharge the projectile (physiological response), hit the mark (satisfaction of the organic need). All of the factors may be related as members of a simple mechanical causal sequence except the aim. For this in our illustration a glance backward is necessary. An adaptive simple reflex is adaptive because of a pre-established series of functional sequences which have been biologically determined by natural selection or some other evolutionary process. This gives the reaction a definite aim or objective purpose. In short, the aim, like the gun, is provided by biological evolution and the whole process is implicit in the structure-function organization which is characteristic of the species and whose nature and origin we need not here further inquire into.

Now passing to the more complex instinctive reactions, so far as these are unconscious automatisms, they may be elaborations of chain reflexes of the type discussed above (Loeb). But the *aim* (biological purpose) is so inwrought into the course

of the process that it cannot be dissociated. Each step is an integral part of a unitary adaptive process to serve a definite biological *end*, and the animal's motor acts are not satisfying to him unless they follow this predetermined sequence, though he himself may have no clear idea of the aim.

These reactions are typically organic circuits. The cycle in some of the instincts of the deferred type comprises the whole life of the individual. In other cases the cycle is annual (as in bird migrations, etc.), diurnal or linked up with definite physiological rhythms (e.g., the nidification of birds as described by F. H. Herrick[3]). In still other cases there is no apparent simple rhythm. But always the process is not a simple sequence of distinct elements, but rather a series of reactions, each of which is shaped by the interactions of external stimuli and a preformed or innate structure which has been adapted by biological factors to modify the response to the stimuli in accordance with a purpose, which from the standpoint of an outside observer is teleological, i.e., adapted to conserve the welfare of the species.

Every intelligently directed response to external stimulation involves a large measure of highly complex unconscious cerebration of this type; and it is possible to describe with considerable precision the mechanisms of the subcortical activities involved in many of those organic circuits which are commonly regarded as typically cortical.

Much of that which goes in psychological literature under such contradictory terms as unconscious mind or subconscious mind is in reality the subcortical elaboration of types of action system which ordinarily do not involve the cortex at all but which upon occasion may be linked up with cortical associational processes and then come into consciousness in such a form as to suggest to introspection that they are all of a piece with the conscious process with which they are related. In fact, within the cortex itself there are doubtless many routine activities which do not ordinarily come into consciousness, particularly of the sort known as acquired automatisms or lapsed intelligence; and these, though of quite different origin from the innate instinctive systems, cannot easily be distinguished from them in the form in which they are experienced in the adult.

[3] *Science*, N. S., vol. 25, 1907, pp. 725-726 and 781-782.

In the organic circuit as defined by Dewey the process is considered as a whole so that the response is conceived as logically implicit in the stimulus. The motor reaction, he says, is not merely *to* the stimulus; it is *into* the stimulus. "It occurs to change the sound, to get rid of it." "What we have is a circuit, not an arc, or broken segment of a circle. This circuit is more truly termed organic than reflex, because the motor response determines the stimulus, just as truly as sensory stimulus determines movement." This notion, which is difficult for the practical scientific mind to understand, is considerably clarified by some neurological considerations.

From the standpoint of the cerebral cortex considered as an essential part of the mechanism of higher conscious acts, every afferent stimulus, as we have seen, is to some extent affected by its passage through various subcortical association centers (i.e., it carries a quale of central origin). But this same afferent impulse in its passage through the spinal cord and brain stem may, before reaching the cortex, discharge collateral impulses into the lower centers of reflex coördination, from which incipient (or even actually consummated) motor responses are discharged previous to the cortical reaction. These motor discharges may, through the "back-stroke" action, in turn exert an influence upon the slower cortical reaction. Thus the lower reflex response may in a literal physiological sense act *into* the cortical stimulus complex and become an integral part of it.

But there is another aspect of the problem which has recently been brought to our notice by Kappers.[4] It is a well known fact, which is not often taken account of in this connection, that the descending cortical paths (central motor bund es) do not typically end directly upon the peripheral motor neurones whose functions they excite, but rather upon intercalary neurones which lie in the reticular formation or even in the adjacent sensory centers. These intercalary neurones in turn excite the peripheral motor neurones. The same intercalary neurone which receives the terminals of the pyramidal tract also receives collaterals from the peripheral sensory neurones of its own segment (Fig. 4). This arrangement is the explanation of the fact that

---

[4] Kappers, C. U. Ariëns. Ueber die Bildung von Faserverbindungen auf Grund von simultanen und sukzessiven Reizen. Bericht über den III. Kongress für experimentelle Psychologie in Frankfurt a. Main, 1908. Also, Weitere Mitteilungen über Neurobiotaxis. Folia Neuro-Biologica, Bd. I, No. 4, April, 1908, pp. 507–532.

the pyramidal tract fibers descend through the human spinal cord for the most part in the dorso-lateral columns, not in the ventral columns like most other motor tracts. In most lower mammals the pyramidal tract actually descends within the dorsal funiculus in the closest possible association with the peripheral sensory fibers, and this arrangement is clearly the primitive relation of the descending cortical pathway.
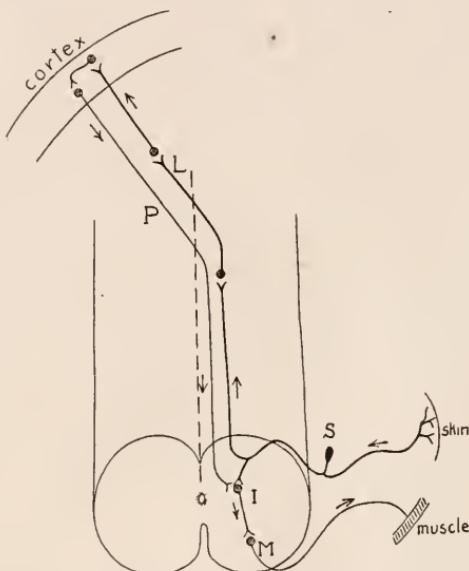
FIGURE 4. Diagram of the relations of the pyramidal tract in a rabbit or similar lower mammalian brain. Sensory stimuli enter the spinal cord from the skin through the peripheral sensory neurone, S, and ascend to the cerebral cortex through the lemniscus, L. The descending pyramidal tract, P, lies in the dorsal funiculus of the spinal cord. Its intercalary neurone, I, may be stimulated by both the peripheral neurone S and by the pyramidal tract P. It discharges upon the peripheral motor neurone, M.

Accordingly, stimulation of the skin of the body excites a dorsal spinal root fiber which ascends toward the cortex within the spinal cord and also gives collateral branches to intercalary neurones of the spinal cord itself. The latter neurones may excite motor elements of the spinal cord to an immediate reflex response which is well under way before the cortical return motor impulse gets back to the spinal cord and discharges into these same intercalary neurones which are already under sen-

sory stimulation directly from the periphery.   The effect of
this arrangement is that the central motor path during function
is under the influence of sensory stimulation at both ends, and
is not, as commonly described, under simple sensory stimula-
tion at the cortical end and purely emissive in function at the
spinal end.

Viewed from the standpoint of cerebral dynamics, the exact
physiological effect of the discharge of a central motor bundle
such as the pyramidal tract will be dependent upon the com-
bined action of the sensory stimulation at the cortical end and
the state of sensory excitation at the spinal end, as well as
upon the resistance of the motor apparatus itself.

We saw in a previous paragraph how the simple reflexes of
the spinal cord may become factors in the stimulus complex
of the cortex.   Here we find, conversely, that the efferent cor-
tical discharge may become a factor in the local reflex stimula-
tion of a motor spinal neurone.   From both standpoints, Dewey's
conception of the unitary nature of the organic circuit, as con-
trasted with the classical reflex arc concept, receives strong
support.

The thalamic association centers probably serve as the organs
par excellence where are elaborated those organic circuits which
give to the higher apperceptive processes of the cortex that
quale to which Dewey refers.   The origin of this quale is to be
sought partly in the subcortical assimilation of a present stim-
ulus complex to the pre-existing organic circuits structurally
laid down in the reflex mechanism, and partly in an affective
quality pertaining to the several organic circuits involved in
the reaction.   This affective quality may be innate or it may
have been acquired by experience of the results of previous
reactions of the sort in question.

Head and Holmes[5] have brought forward some very inter-
esting evidence that not only the affective quale of sensations,
but also the emotional life in general, is functionally related to
the primitive intrinsic nuclei of the thalamus, rather than to
cortical activity.   And certainly there is much evidence in the
behavior of lower animals, especially birds, that a high degree
of emotional activity is possible where the basal centers are

[5] Brain, vol. 34, p. 255, 1911.

highly elaborated but the cerebral cortex is small and very simply organized.

From all of these considerations it seems probable that the functions of the higher association centers of the cerebral cortex do not consist of the elaboration of crude sensory data or of any similar elements, but rather of the coördination and integration of highly elaborated subcortical organic circuits which in the aggregate make up the greater part of the reflex and instinctive life of the species.

NOTES

MEASURED ELECTRICAL STIMULI IN THE STUDY OF BEHAVIOR

ROBERT M. YERKES

The Martin method of measuring induction shocks has now been perfected to a point which renders it available for students of animal behavior and it seems wholly desirable that all who are engaged in this field of research should familiarize themselves with Dr. Martin's recently published book on this subject [1]

As the author remarks in his introduction, "There are few physiological researches which do not involve artificial stimulation of tissues; and for the production of stimuli induction shocks are in most cases the first choice. They are easier to use and they subject the stimulated tissue to less permanent modification than do other forms of artificial stimulus. Induction shocks are, however, very variable in intensity; and as commonly used there is no means of knowing or of stating their physiological effectiveness in other than the most general terms. An induction shock is weak, medium, or strong. More closely than that the user does not attempt to describe it.

"This lack of knowledge as to the strengths of the stimuli employed is often a serious handicap in the prosecution of individual researches, particularly such as call for the use of stimuli of varying strengths. It also operates to make uncertain the attempts of investigators to duplicate the experiments of others.

"No one will question the desirability of being able to measure faradic stimuli, both for the sake of controlling the stimuli used in one's own experiments, and also in order that these stimuli may be so described as to enable other workers to duplicate them as occasion arises.

"The purpose of this work is to outline a system for calibrating the apparatus used in generating induction shocks, so that

---

[1] Martin, Ernest G. The Measurement of Induction Shocks; A Manual for the Quantitative Use of Faradic Stimuli. New York: John Wiley & Sons, 1912, pp. vii + 117.

the value of the shocks may be expressed in terms of stimulation units; these units to be applicable to any properly constructed induction apparatus, and to be based upon determinations which can be made in any ordinarily equipped physiological laboratory. The system proposed is not a new departure, but is an extension and amplification of previous systems." (l.c., p. 1 and 2.)

These statements apply to many investigations in behavior and psychology as well as to more strictly physiological investigations. Dr. Martin's method is sufficiently simple to render it easy to use and it should be carefully considered by all investigators who desire to do accurate work.

THE NATURAL HISTORY OF BIRDS

ROBERT M. YERKES

Of the thirteen volumes in the new (fourth) edition[1] of Brehm's justly famous history of animals, three of the four volumes devoted to birds have been issued. They are numbered as volumes 6, 7 and 8 in the set. All bear the date 1911, and each volume is available in half leather at the very reasonable price of 12M ($3.00).[2]

The greater part of the materials constituting the fifteen hundred pages of these volumes were gathered and prepared for publication by the late Professor William Marshall whose death in 1907 left his great task to be completed under the direction of Doctor F. Hempelmann. In his preface to the volumes, Doctor Hempelmann especially calls attention to the emphasis which has been laid, in this revised edition, upon the structural characteristics of birds and upon their systematic relations. Chief responsibility for the facts of bird behavior and psychology is placed upon the general editor, Professor Otto zur Strassen.

The first fifty pages of volume one offers an admirably clear, concise, and complete description of the structure of the bird, of its development, its general habits, instincts, intelligence and systematic relations. Thereupon follow descriptions of the various orders, suborders and families of birds.

Throughout the volumes, the text is admirably illustrated by hundreds of wood cuts, half tones, and colored plates. Neither labor nor expense has been spared in the preparation of text and illustrations.

The accounts given of representatives of the various divisions of the class aves are interesting throughout and they appear to be reliable. Naturally, the work does not give detailed infor-

---

[1] A descriptive notice of this edition appeared in this Journal, vol. 1, pp. 307–8.
[2] Tierleben, Sechster Band. Die Vögel, Erster Band: Flachbrustvögel, Tauch-vögel, Pinguinvögel, Sturmvögel, Storchvögel, Gänsevögel, Raubvögel. Leipzig und Wien, Bibliographisches Institut, 1911, S. xvi + 498.
Tierleben, Siebenter Band. Die Vögel, Zweiter Band: Steiszhühner, Hühner-vögel, Kranichvögel, Regenpfeifervögel, Kuckucksvögel (Kuckucke). Leipzig und Wien, Bibliographisches Institut, 1911, S. xiv + 492.
Tierleben, Achter Band. Die Vögel, Dritter Band: ¡Kuckucksvögel (Papageien), Rakenvögel. Leipzig und Wien, Bibliographisches Institut, 1911, S. xii + 472.

mation concerning all of the birds which are mentioned, but it gives valuable general information concerning a very large number of types of bird, and one may turn to these volumes for general information concerning the natural history of this group of organisms with the certainty of acquiring a large amount of useful information and of being stimulated to further study of the form and behavior of organisms.

From the point of view of the reviewer, the editors of these volumes richly deserve commendation for their intelligent and thoroughly conscientious rewriting of this portion of the great natural history. It is a work which should be rendered available in several languages. In English, we have nothing at all comparable to it and, as was suggested in our preliminary notice of the new edition, it is very much to be desired that the complete work be rendered into English.

BEHAVIOR OF RACCOONS TO A TEMPORAL
SERIES OF STIMULI

F. M. GREGG AND C. A. McPHEETERS

From the Psychological Laboratory of the University of Chicago

Four figures

This problem was suggested by, and the experiments were conducted under, the supervision of, Dr. W. S. Hunter. In his thesis on Delayed Reaction, Dr. Hunter found it necessary to criticise all extant arguments and experiments designed to prove the existence of images in animals. One of the most striking of these experiments is that of Cole,[1] in which raccoons were taught to discriminate between two temporal series of stimuli. It was proposed that we repeat this particular experiment and test some of its conclusions and assumptions in the light of additional control tests.

Cole's apparatus was termed a "card displayer" and his diagram is duplicated in figure 1. It consists of three levers, with cards attached, mounted on a common axis inserted in the rear of a 12-inch board which serves as a screen. By the operation of the lever mechanism, these cards can be raised above the board and displayed as stimuli to the animal. The cards used were white, blue and red. In what may be termed the positive group or series, white, blue and red were displayed in succession, and the animals were taught to react to this temporal series during the presentation of the red card by mounting the steps shown in the diagram. Food was the reward of a successful response. In the negative series, the red

[1] Cole, L. W. Concerning the Intelligence of Raccoons. *Jour. of Comp. Neur. and Psych.*, 1907, vol. 17.

card was exhibited three times in succession; the animal was taught to respond during the third presentation, and the response consisted of an inhibition, i.e., the animal must remain off the steps. This inhibitory response was inculcated without a food reward.

Three animals learned the discrimination, and Cole makes three questionable assumptions as to *facts:*—(1), The discrimination was mediated through vision; (2), it was based upon card distinctions (presumably differences in color and brightness), and (3), all three presentations of each series were effec-
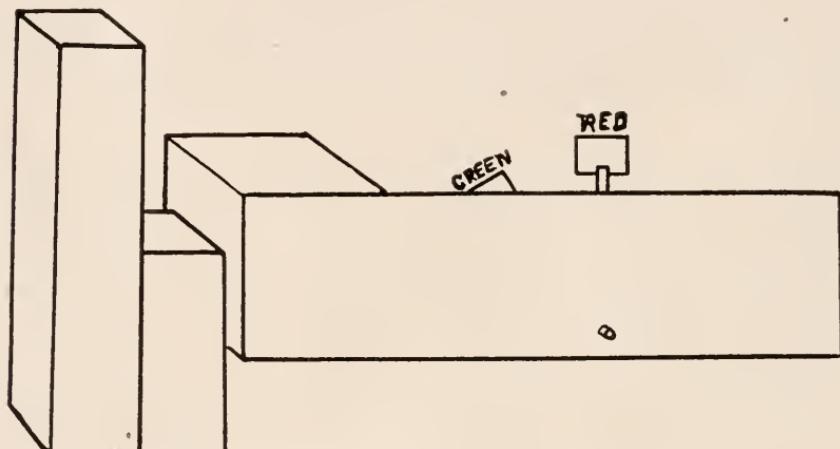
FIGURE 1.   Dr. Cole's color-displaying device and feeding block

tive components of the stimulus. His evidence upon this latter point consists of the fact that the response generally occurred during the presentation of the third card. Since this third member was identical for the two series, it, in and of itself, could furnish no basis for the two differential responses. In case of premature responses, i.e., attempts to mount the steps before the third card was presented, Cole observed that the animal frequently stopped and looked around when this final card was presented. This behavior indicates that the final red card "was not a neglected element of the situation."

The argument in favor of the existence of images takes two forms and each involves a questionable assumption of *theory:*—

---

[2] Op. cit., p. 258.

(1), In normal behavior the responses occur during the presentation of the third card which is common to both series. The responses must then be determined in part by the preceding cards which are no longer present to sense. Hence the *stimulat-*
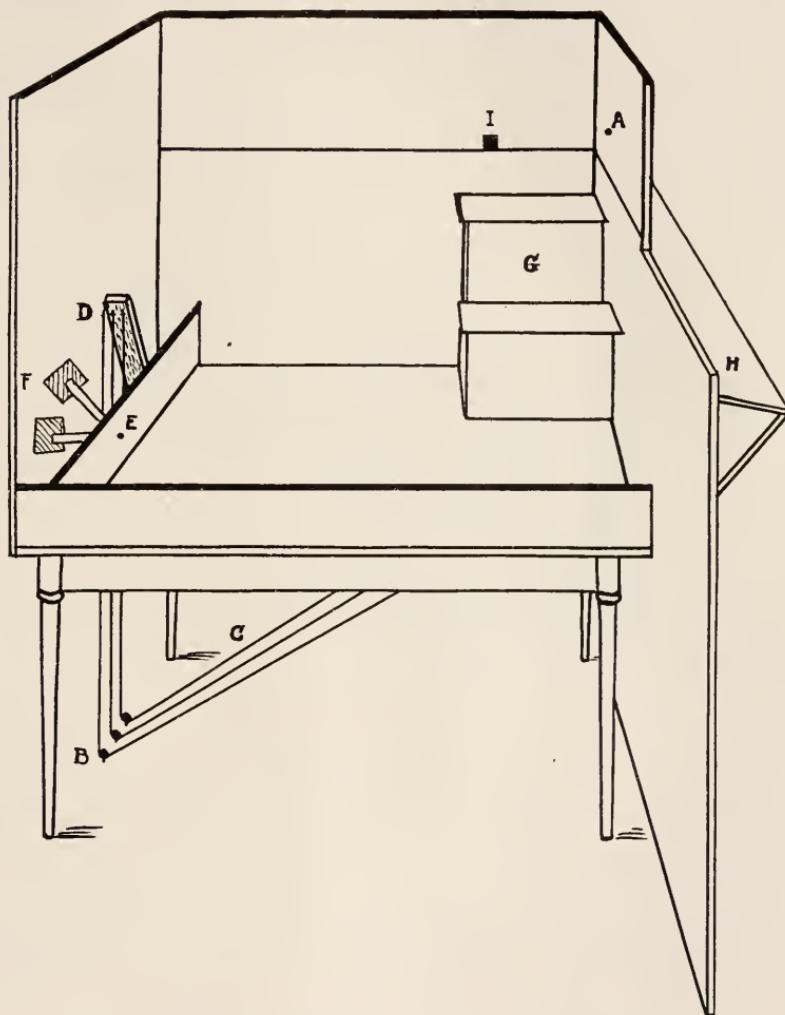
FIGURE 2. Gregg and McPheeters' experiment table and apparatus

ing effects of the first two cards of each series must be *carried over* in some manner until the response does occur. The questionable assumption is now made that this "carrying over" function can be subserved only by an imaginal process. (2),

With the premature responses, the "turning back" proves not only the effectiveness of the final card, but it is assumed that this behavior was *instigated* by an anticipatory image of that card. We are told that this final red was an anticipated and expected color "which they (the animals) generally waited to see but sometimes were too eager to wait for."[3]

The essentials of Cole's apparatus and method were duplicated in our experiment. The main difference consisted of the introduction of a large screen to hide the experimenters. Our apparatus is represented in figure 2. Our operator, usually Mr. Gregg, stood at the rear right hand corner of the table and observed the raccoons through a 1 cm. opening, A. He manipulated the levers, F, by pulling the cords, C, which passed from the ends of the levers down through pulleys on the floor, B, and up to a point within easy reach of his right hand. The levers were limited in their range of movement by elastic cords, D, attached at their lower ends to the table and at their upper ends to an upright bar. This arrangement kept the levers hidden when not in use, and reduced the noise of the operation to a minimum. The board screen, E, was about five inches high. The color cards, F, were two inches square, and when elevated above the board they were practically on a level with the eyes of the raccoons. The distance between the elevated positions of contiguous cards was approximately one-half inch. The levers were similar in form, size and appearance. The distance between the levers and the feeding steps, G, was two feet. The observer and recorder, usually Mr. McPheeters, stood at the shelf at the front and right end of the table. All of his body with the exception of his head was screened from the view of the animals.

The positive series consisted of white, blue and red cards presented in immediate succession. Mounting the steps was considered a successful response and this reaction was rewarded by a morsel of food received through the hole, I. Figure 3 represents Jill in the act of feeding. Any tendency to premature response in this series was punished by the withholding of food. The red card presented three times in succession constituted the negative stimulus. Remaining off the steps was regarded as a successful response, but no food was given either

---

[3] Op. cit., p. 258.

for successful or unsuccessful reactions to this stimulus. The experiment offered no means of punishing premature responses in this series.

Two raccoons were used in these experiments, a male, Jack, and a female, Jill. These animals had been previously employed in Hunter's experiments on Delayed Reaction. No factors essential to the solution of the problem were carried over from their previous training. The raccoons were docile, and, after a preliminary period of feeding upon the table, manifested no fear of the apparatus or experimenters.
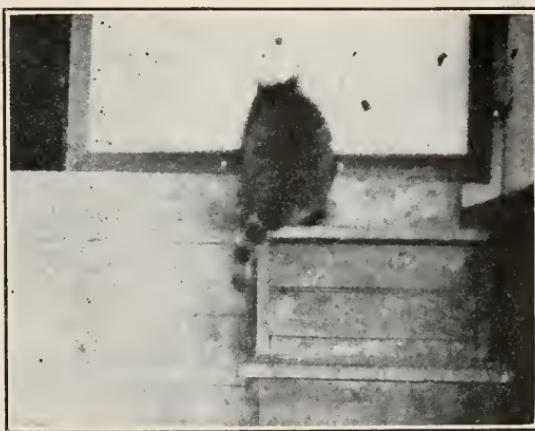
FIGURE 3.   Jill in the act of feeding

LEARNING SERIES

The animals were taught to react to the positive series (W-B-R) and to inhibit reactions to the negative series (R-R-R) in the following manner:—(1), They were fed for one week upon the experimental table to accustom them to the novel surround'ngs. (2), They were now taught that food could be obtained only through the screen opening (I) after mounting the steps. (3), In two days they learned to respond whenever the levers (without cards attached) were presented. The animals reacted immediately to the first stimulus resulting from the operation of the lever mechanism. (4), Color cards were attached to the levers and only the positive series (W-B-R) was presented. The animals were forced to delay their response until the complete series was given. Food was withheld for

all premature responses. Fifteen days were necessary to inculcate this habit so that 80% of correctness was secured. (5), In the final stage the negative series (R-R-R) was introduced and two weeks was allowed to learn the discrimination between the two series. At first the positive series was presented the more frequently. As the learning progressed, the two series were presented an equal number of times. The two series were alternated in a definite complicated order. The number of trials per day varied from 30–50 according to the condition of the animals. Typical records at the beginning and at the end of the learning period are :—

	Jack		Jill	
	Trials	Accuracy	Trials	Accuracy
Positive series...................	27	89%	31	84%
Negative series...................	14	29%	17	24%
Positive series...................	19	95%	22	91%
Negative series...................	20	0%	22	91%

There was no discrimination at first. Both animals reacted to the negative series almost as frequently as to the positive series. Jack's training had simply perfected his reaction to any *completed* series. Further training *might* have developed discriminative reactions in his case, but time did not permit a continuance of the tests. Jill, on the other hand, easily mastered the problem and discriminated between the two series on some basis.

Several peculiarities of behavior were evident during the learning. (1), During the fourth stage, the animals began to seek cues from the experimenters. This was particularly true of Jack. He seemed to watch the peep hole, although possibly he was merely listening for some sound upon which to base his reactions. The slightest rustle or movement on the part of the operator was sufficient to initiate a response. This conduct was most evident during the interval between stimuli, or immediately after the presentation of the third card. In order to eliminate this extraneous cue, a metronome was kept beating at a rate of 80 vibrations per minute during the tests. This noise was sufficient to render inaudible the slight sounds made by the operator as we had no further difficulty from this source. (2), The behavior which Cole emphasizes so strongly occurred very frequently. The animal reacts prematurely, hesitates,

and then turns to look for the third stimulus. (3), During the fourth stage, the animals acquired their fixed modes of behavior. Jack always stood at a position of 6–10 inches from the nearest lever. This position during the presentation of the levers is illustrated in figure 4. Jill, however, soon acquired the habit of standing close to the levers and touching her nose to them as they appeared. (4), When the final stage of discrimination was introduced, Jack's behavior did not change. Very seldom did he inhibit a response. He either reacted prematurely or else reacted at the end of every series whether positive or negative. (5), Very significant changes occurred in Jill's behavior.
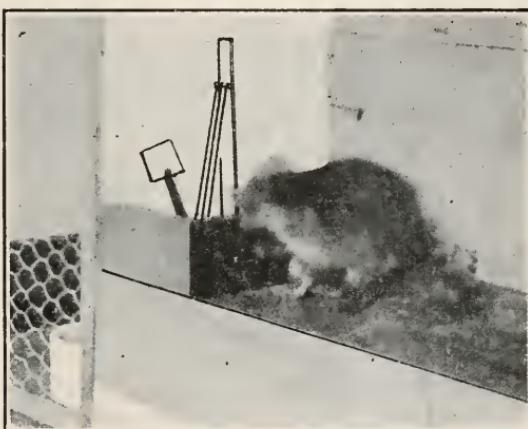
FIGURE 4. Jack in the stimulus position

She soon learned to react immediately after the first presentation of the negative series. Very rarely did she wait for the second card but turned and walked unconcernedly about the table as soon as the first card was presented. Since no food was given in the negative series, the conditions of the experiment offered no means of punishing this prematureness of response. With the positive series, Jill became highly impatient to react immediately after the appearance of the first card, and in fact many premature responses did occur. In this series, however, every premature response was punished by the withholding of food. In all probability immediate reaction to the first card would also have developed in this series if punishment had not prevented. This behavior indicates that the discrimination was

based primarily, if not wholly, upon the initial members of the two series.

CONTROL SERIES

Jack failed to discriminate between the two series, but he did learn to inhibit his responses until the final card had appeared. The control series of tests was instituted to determine the stimulus of these responses. (1), The color cards were removed and the levers alone were presented. No disturbance of normal conduct resulted. (2), The levers were so operated that they made their usual sound while they did not appear above the screen board. The visual-auditory stimulus was thus replaced by an auditory one alone. No change in behavior resulted. (3), A series of but two sounds invariably stimulated the normal response. When a series of four or five sounds were given, Jack always inhibited his reaction until they ceased. Since all possibility of contact stimuli is eliminated by the distant position of the animal from the levers, these controls indicate that *any completed* series of sounds constitutes the sensory stimulus for this raccoon.

To determine the basis of Jill's discriminative reactions, it was necessary to proceed cautiously for fear of destroying or radically altering the coordination. Because of the crucial importance of these tests, they will be described with some detail in the order in which they were given.

1. To test the relative efficiency of color *versus* lever order, the red and white cards were interchanged. The normal order of colors was given and as a consequence the order of lever positions was reversed from that of the normal. Hereafter in describing the order of lever positions, they will be numbered according to their distance from the animal. The results are given in the table.

Stimulus	Positive responses	Inhibitions
W-B-R, 3-2-1	31	9
W-B, 3-2 (premature)	8	
R-R-R-, 1-1-1	17	14

Counting the eight premature responses as correct, we have a percentage of 67 in 79 trials on the assumption that the reactions were made to *color order*. These results are very poor as compared with previous records. On the preceding day the percentage of correct behavior was 91, and the average per-

centage for the six preceding days was 87. Evidently there is some connection between "lever order" and the ability to react correctly.

2. The normal order of colors and levers gave an accuracy of 87% for 15 trials, which is a normal record.

3. Mr. Hunter operated in the place of Mr. Gregg, and secured an accuracy of 86% for 7 trials with the positive series and a percentage of 89% for 9 trials with the negative series.

4. Mr. Gregg operated, the levers were washed, fresh color cards used, and the normal order of presentation was given. Nine trials gave an accuracy of 89%.

5. The red and white cards were again interchanged in position, and the two series consisted of R-B-W, 1-2-3, and R-R-R-, 1-1-1. The animal was fed whenever it chose to react to either series. Both series stimulated positive responses. Discrimination was absent. There were but two inhibitions in 16 trials and both of these were in response to the R-R-R series.

6. The normal color and lever order was given and a discriminative accuracy of 93% was secured in 15 trials.

7. Mr. McPheeters operated in the place of Mr. Gregg, as the latter still retained a suspicion that the animal might be reacting to some difference in his method of giving the two series. The normal color and lever order was adhered to. An accuracy of 90% in 10 trials was secured.

8. The normal lever order of 1-2-3, and 3-3-3 was given, but the positions of the cards were so shifted that the colors were presented in the order cf R-W-B, and B-B-B. Jill was fed only after response to the series R-W-B. Assuming that the discrimination was based upon differences of "lever position," this test gave an accuracy of discrimination of 90% in 20 trials. Evidently the shift of presentation order of the cards did not disturb the discriminative reactions in the least.

9. Violet, green and yellow cards were substituted for the white, blue and red cards respectively. The normal lever order was adhered to. This change rendered both series different from the normal in color and brightness. No disturbance in behavior resulted. The two series were discriminated successfully in 86% of 21 trials.

10. The cards were now removed and the bare levers were presented in their normal order. The animal successfully dis-

criminated between these two groups of lever positions in 88% of 17 trials.

11. The three levers were practically identical so far as form, size and appearance are concerned. To test the possibility that the levers were distinguished on the basis of their individuality as tactual or visual objects, rather than on the basis of their positional differences, the levers were interchanged in position. Lever 1 was placed in the second position, lever 2 in the third position, and lever 3 was given the first position. The cards were removed, and the normal order of position was given. No disturbance resulted.

12. The original series, both of colored cards and of lever order was alternated throughout two days' experimentation with a series in which the cards were removed but the normal lever order maintained. These tests were introduced to substantiate more thoroughly the contention as to the ineffectiveness of the cards. The tests prove that the presence of the cards is not only unnecessary for discrimination but also that their presence does not materially increase the accuracy of that discrimination. An accuracy of 94% was secured for 55 trials when the cards were present. Absence of the cards gave a percentage of 92 for 53 trials.

13. This test was designed to determine whether the "positional" difference between the two temporal series of lever presentations was apprehended by means of vision or touch. The color cards were used and the normal lever order was maintained. A plate of window glass 18 x 24 inches was placed immediately in front of the levers. This glass effectually prevented all contact, ·but it in no way disturbed vision. The animal was allowed 20 minutes to become accustomed to the new situation. Neither timidity, nervousness, nor curiosity were manifested. During the two days' experimentation, tests were taken both with and without the presence of this glass, all other conditions remaining constant. Without the glass, behavior remained normal in every respect. The presence of the glass, however, destroyed the coordination. The animal's attitude was one of bewilderment. The first 11 trials were all incorrect. The raccoon soon learned to react either to the visual appearance or noise of the levers, but she responded to every presentation, both positive and negative. In other words inhibition to the negative series ceased; discriminative ability was destroyed.

The above series of tests prove rather conclusively that (1), the animal was not dependent upon the operator's method of manipulating the lever mechanism; (2), neither the brightness, color nor presence of the cards are necessary to the discrimination; (3), the animal is not reacting to individual peculiarities of the levers; (4), the discrimination is based primarily upon an apprehension of a difference of spatial position between the two groups of levers; (5) this apprehension of the spatial difference between the two groups is not mediated through the olfactory, auditory, or visual modalities of sense; (6), this difference between the two lever groups was perceived by means of nose contact, for, (a) all other sensory possibilities were eliminated, (b) nose contact was present throughout the tests and (c) discrimination failed completely when such contact was prevented; (7), the discrimination was based upon active rather than passive touch. The animal did not hold the head in a constant position and allow the ascending levers to strike at a series of positions on the cheek. The head was moved so as to receive each contact upon the nose. As a consequence, we are forced to infer that the kinaesthetic sensitivity involved in reaching for the stimulus was probably more effective than pure contact in these discriminative responses.

14. The positional difference between the levers upon which the discrimination was based was one-half inch. The thickness of the levers was one-quarter inch. Levers made of thin sheet iron were now substituted. By the use of washers the above positional differences were maintained. A series of 117 trials gave an accuracy of 90%. Most of the errors occurred in the negative series and during the early trials. The change of material and thickness of the levers thus produced, as might be expected, a slight temporary disturbance which was soon eliminated.

15. The positional difference was now reduced to a minimum by removing the washers between the thin sheet iron levers. The purport of the control is obvious. The experiment, however, was not satisfactory as the levers would catch and bind, and time was consumed in disengaging them. The animal soon became confused, excited and impatient to react. The significance of the results is thus ambiguous. Irrespective of their interpretation, the factual results are:—the percentage of pre-

mature responses was significantly increased, the positive series was reacted to correctly, while the negative series gave more positive than negative responses. Such results might naturally be expected from the animal's excitement and impatience. In the few cases where the levers worked smoothly and the animal seemed in a normal mood, discrimination failed for the minimum of spatial difference. However, we must confess that our test was not decisive.

16. A final series of tests covering three days of experimentation was given (1) to determine the composition of the two lever groups which renders them effective as specific stimuli, and (2) to determine the relative effectiveness of the three members constituting any lever group. Since the cards are ineffective, they were not removed. Dr. Hunter operated in the enforced absence of Mr. Gregg. The results are given in the following tabular statement.

Stimulus	Positive	Inhibitions	Percentage of discrimination
W-B-R (1-2-3)......................	44	2	
R-R-R (3-3-3)......................	5	27	91.
W-W-W(1-1-1)......................	13	0	
R-R-R (3-3-3)......................	1	13	96.
W-R-R (1-3-3)......................	11	0	
R-R-R (3-3-3)......................	1	9	95.
B-B-B (2-2-2)......................	6	0	
R-R-R (3-3-3)......................	1	3	90.
W-W-W(1-1-1)......................	25	0	
B-B-B (2-2-2)......................	6	14	87.
W-B-B (1-2-2)......................	23	5	
B-B-B (2-2-2)......................	4	13	81.

As to the character of a group constituting a specific stimulus we may say:—(a), The group is highly general, never definite and particular. Positive reactions of food getting may be stimulated successfully by any of the following groups— 1-2-3, 1-3-3, 1-2-2, 2-2-2, or 1-1-1. Likewise, inhibition, or negative responses, may be stimulated by either group 3-3-3, or 2-2-2. (b), The nature of either stimulus is relative to the character of the other group with which it is alternated. The group 2-2-2 may serve equally well either as a positive or negative stimulus. It excited the negative response with an average

correctness of 73% in two of the above series; it likewise func-
tioned on one occasion in inducing positive responses with a
correctness of 100%. (c), When two groups are alternated,
that nearest to the animal serves as a positive stimulus, while
the more distant one becomes the negative stimulus. The
group 2-2-2 was positive when alternated with 3-3-3, but it
functioned negatively when given in conjunction with 1-1-1.
(d), The effectiveness of any two groups in inducing differential
responses is proportionate to their distance apart. The groups
1-1-1 and 3-3-3 were discriminated with an accuracy of 96%
for 27 trials, while the above two groups were distinguished
from 2-2-2 with an accuracy of but 87% for 55 trials.

The above principles may be stated in terms of positions as
follows:—When two groups of positional stimuli are alternated,
the one nearest to the animal becomes positive while the more
distant one is negative. The accuracy with which the two
groups may be discriminated is proportional to the degree of
depth distinction between them. The animal thus responds to
objects according to their relative position in depth.

As to the relative effectiveness of the three members com-
prising any group stimulus, our results indicate with a high
degree of probability the following conclusions:—(1), The dis-
crimination *can* be based *exclusively* upon the difference between
the first members of the two groups. Only these initial factors
were effective in a majority of the tests. This conclusion is
founded upon several groups of facts. In no. 16 of the control
tests, 66 trials were given in which the last two members were
identical in the two discriminated groups, yet these trials gave a
discriminative accuracy of 85%. Moreover, this accuracy was
proportionate to the degree of space difference between the
two first members; for example, the groups 1-3-3 and 3-3-3
gave an accuracy of 95% as compared with a percentage of
80 for such groups as 1-2-2 and 2-2-2. When two groups are
identical as to the first member but different in respect to the
last two positions, discrimination is impossible. In no. 5, the
groups 1-2-3 and 1-1-1 were distinguished in but 12% of the
trials, a record which can be accounted for on the basis of
chance. As before noted, the discrimination was mediated
through contact and the first member of each group was usually
nosed. The inhibitory response to the negative series was

finally made *immediately* after the first presentation. With the positive series, the animal became impatient to react after the first presentation and in fact many such premature responses did occur. In all probability immediate reaction to the first member would also have developed if this tendency had not been punished by the withholding of food. (2), The final member was never effective in the discrimination. The conclusion is supported by the facts already cited as to the tendency to correct premature responses to the positive group, and the usual reaction after the first presentation of the negative group. This third element was common to the two groups in the original experiment, and logically it is obvious that a common element can not serve as a basis of distinction. This training on the original series would naturally tend to make the animal neglect this final member in those cases where it did offer a possible basis for discrimination. As a matter of fact those groups which did differ as to the third component gave a discriminative accuracy no higher than the normal. (3), While the third member is useless so far as discrimination is concerned, yet it did possess a function in the positive group. As Cole asserts, this component "was not a neglected element of the situation." [4] It functioned, however, merely to *release* the discriminative response which had already been aroused by the preceding members of the group. (4), As to the efficacy of the second member, our results are far from conclusive. Exigencies of time at the close of the college year prevented an adequate completion of the tests. The facts as to premature responses indicate that this element was sometimes effective in the positive series, but that it constituted no part of the negative stimulus. In test no. 5, the groups 1-1-1 and 1-2-3 were both regarded as positive stimuli, but the percentage of responses was slightly greater in the latter case. This fact indicates a slight effectiveness of the second element. Some results of test no. 6 corroborate the assumption. A comparison of the last two groups shows that the accuracy of discrimination is slightly greater when the two series are different as to the second member than when they are identical in this respect.

The conclusions thus far advanced are consonant with all of the facts except those of the first control test. With the

---

[4] Op. cit., p. 258.

groups 3-2-1 and 1-1-1, we would expect a high degree of discrimination, with the group 1-1-1 being regarded as the positive stimulus. As a matter of fact the animal was confused and unable to give consistent results. Both stimuli were sometimes regarded as positive and sometimes as negative, though the tendency to a positive selection was the stronger in both cases. The group 3-2-1, however, was selected as positive much more frequently than was the group 1-1-1. These results offer three possibilities of interpretation:—(a), An animal may adapt itself to the alterations of the discriminative stimuli which are introduced in the control tests. In this way the nature of the effective stimulus may be gradually altered. By interpolating but a few controls in a longer series of the normal, one can prevent any radical alteration except as to some minor details. For example, much of the relativity of the two group stimuli in our experiment was probably acquired during the controls. The anomalous results of the first test can be explained upon the hypothesis that the discrimination was originally based upon both color and lever order, the breakdown was due to the functional opposition of the two factors, and the element of color order was subsequently neglected. There are several objections to such a hypothesis. The visual element must have been stronger than the factor of position to account for the strong positive tendency in the responses, and it is improbable that the stronger component should be subsequently neglected. The change or adaptation should be gradual and there is no evidence of this. The animal which stood in such a position that lever contact was impossible failed to learn the discrimination on a visual basis. (b), The first alterations of any accompanying conditions upon which the discriminative responses do not directly depend may cause confusion and disturbance and the animal may soon learn to adapt itself to these novel disturbing conditions. There was much in the behavior of the raccoon which suggested such a hypothesis. (c), The results may also be explained by additional assumptions as to the nature of the group stimuli, which in no way conflict with our previous conclusions. We may assume that both the first and second members of the group are sometimes effective, that the animal tends to react positively to any spatially distinct series of stimuli, and negatively to any series of identical members. While,

as we have asserted, the two groups are relative to each other, yet they cannot be completely relative. The stimuli must also possess certain fixed, definite and absolute attributes and this feature is furnished by the above characteristics of difference or identity of component elements. The group 3-2-1, given in conjunction with 1-1-1, would be selected as negative so far as the animal was depending upon the factor of relativity of depth distinctions, but it would likewise be regarded as positive in so far as the animal was influenced by this definite characteristic, viz., a series composed of different elements. The anomalous results of the first test are thus explicable on the assumption that the two effective factors of each group stimulus were brought into antagonism. In the normal series, one stimulus invariably consisted of a succession of identical elements (3-3-3), while the other stimulus was invariably composed of a succession of different elements (1-2-3). One has a right to assume that the animal in learning to distinguish the two will rely to some extent upon every available distinctive aspect —upon the factor of identity *versus* difference of elements as well as upon relative nearness or distance of the groups. The writers incline to this hypothesis because it harmonizes with and supplements the conclusions previously enunciated. This explanation of the results of test no. 1 furnishes additional evidence in support of our previous contention as to effectiveness of the second member of the group stimulus.

It is evident from our results that Cole's conclusion as to a discrimination based upon visual peculiarities of the cards is an unwarranted assumption. He did not (so far as can be determined from his account) eliminate the possibility of a discrimination based upon cues from the experimenter, or upon his method of lever manipulation. The discrimination may have been tactual as in the case of our animal. Cole describes his animals as standing with forepaws upon the card displayer and clawing at the levers, and our raccoon which stood in such a position that contact was impossible failed to master the problem. However, we do not wish to make any conclusions as to Cole's animals; we merely wish to point out the naïve anthropomorphism underlying his statement of fact.

His conclusion as to the efficacy of the third lever in the positive series is valid, but he fails to distinguish between a

discriminative and a "releasing" function. We are sceptical as to the efficacy of the final levers in his negative series; in speaking of the negative series, he says "for each one, on seeing the first red, would drop down from a position with both forepaws on the front board to stand on all fours on the floor in front of it and merely glance up at the succeeding reds." [5] Remember that the experiment offered no means of punishing premature responses in this series, and that our animals finally reacted immediately after the first presentation. It is rather difficult to identify a negative or inhibitory response and we see no reason why this climbing down from the card displayer should not be regarded as the negative response.

Our factual criticisms, however, do not invalidate Cole's argument in favor of imagery. His logic applied to our facts would merely substitute kinaesthetic-tactual for visual images. As formerly noted, his two arguments involve theoretical assumptions. (1), His animals as well as ours during the course of a premature response frequently stopped and went back to the card displayer when the third lever was presented. Cole assumes that this behavior was initiated by an image. The assumption has two weaknesses. (a), It is more probable that the act was stimulated by the noise of the lever. The raccoon is very sensitive to sounds and any noise would naturally possess a distractive function. This sound has been an invariable component of the stimulus associated with food satisfaction, and hence it would soon acquire motive power. Punishment of premature responses would strengthen the effect of such a stimulus. The assumption of images to explain such conduct is entirely gratuitous. (b), Granted the existence of images, one may argue with some plausibility that they would function to *prevent*, and not to arouse, the conduct in question. On the assumption that the original function of an image is a substitute for the corresponding sensation in a sensory-motor situation, one would not expect the animal to turn back to secure a sensory stimulus for which it already possesses an adequate substitute. (2), As to the second argument, Cole is correct in maintaining that the stimulative effects of the levers upon which the discrimination was based must have persisted

---

[5] Op. cit., p. 260.

in some fashion until the final presentation was given. This "carrying over" function was probably mediated, not by an image, but by motor attitudes representative of, or associated with the two responses. One can not make positive assertions as to the character of these motor attitudes. One can point out peculiarities of behavior which could well serve such a function. Our animal during the positive series maintained an attitude of tension and excitement, while a degree of relaxation was evident in the negative series. Cole's animals during the positive series remained with forepaws on the card displayer, pawed at the levers and exhibited a state of tension and excitement; with the first presentation of the negative series, they dropped down from the card displayer, maintained an attitude of relaxation and indifference, and casually glanced at the succeeding levers. It is perfectly feasible that two such distinctive motor attitudes might serve as the stimulus or beginning of subsequent appropriate modes of response. If images were present in our animal they must have been kinaesthetic, i.e., imaginal attitudes. Conceived in this manner, the probability in favor of *sensory* attitudes is more convincing. We have described the function of the third lever as one of "release," i.e., we assumed that the first levers determined or initiated the appropriate response, that the conditions of the experiment prevented the immediate completion of the act, and that the final presentation merely released this inhibited movement or motor attitude. This conception is supported by the fact that the animals exhibited a pronounced tendency to immediate or premature responses, a tendency so strong and impelling that punishment never succeeded in wholly eradicating it.

The primary concern of this paper, however, is not to establish any positive doctrines. We expressly refrain from asserting that raccoons can not and do not possess and utilize images. Our purpose is essentially negative and critical; we desire to demonstrate the inadequacy of Cole's experiment as a conclusive and convincing proof of the existence of images. The assumption of higher processes is both unconvincing and futile so long as there exists even the possibility, to say nothing of the probability of an interpretation in terms of lower and more primitive conditions. The existence of images must remain

unproved so long as an experiment, by the absence of appropriate control tests, fails to eliminate the possibility of a " stimulus-response " type of behavior, and we maintain that this possibility of a sensory-motor interpretation of the raccoon's behavior in this discrimination has been rather adequately demonstrated by our tests.

THE OLFACTORY REACTIONS OF THE SPOTTED NEWT, *DIEMYCTYLUS VIRIDESCENS* (RAFINESQUE)

MANTON COPELAND

Bowdoin College

Although olfactory reactions have been recognized in fishes by Baglioni, Parker, Sheldon and Copeland, to my knowledge, no conclusive physiological evidence of a sense of smell in amphibians has yet appeared. In the May-June (1912) number of this Journal, Reese published an article on food and chemical reactions of the spotted newt (*Diemyctylus viridescens*), but failed to show reactions unquestionably dependent on olfactory stimulation. I began a study of the sense of smell in this species two years ago, but was unable to complete it until last summer, while occupying a table at the Laboratory of the United States Bureau of Fisheries at Woods Hole, Massachusetts. I wish to express my thanks to Mr. T. E. B. Pope, Director of the laboratory, for many courtesies received during my stay, and to Mr. P. H. Pope of Manchester, Maine, for his kindness in supplying me with abundant material.

The spotted newt is especially favorable for experimental study as it soon becomes accustomed to life in the aquarium, feeding well, and showing no ill effects from confinement. All my animals were kept in glass aquaria, with sand spread over the bottoms, and were fed from time to time with pieces of raw beef, which were offered.to them on the end of a delicate silver probe.

EXPERIMENTS

As an introduction to the feeding behavior of Diemyctylus, one of my earlier experiments may be described; a series of tests originally planned to throw light on the animal's ability to recognize food. The individual chosen for the tests indicated that it was hungry by seizing and swallowing a piece of raw meat offered it on the tip of a probe. When a ball of white cotton was substituted for the meat, it also was taken into the mouth, but immediately dropped. Another one was seized,

chewed for a while, and discarded.   Instead of testing the ani-
mal again with meat, an extract was prepared by grinding raw
beef in water and filtering the fluid.   A piece of cotton was
then soaked in this juice, and offered the animal as before.
By this procedure the introduction of new visual or tactile
factors was practically avoided, for the color of the cotton was
changed only slightly by the juice.   It was seized, chewed upon
and swallowed.   Plain cotton was then refused.   When the
cotton was moved the newt followed it about, resting the tip
of the snout upon it.   Cotton soaked in juice was then nosed
in a similar way until it dropped off the probe.   When rolled
over the sand, the cotton ball was pursued and again nosed.
Finally it was snapped into the mouth and swallowed.   Plain
cotton, presented to the animal in exactly the same way, was
nosed but not taken.   Lastly, another piece soaked in juice
was offered.   As in the two preceding tests, the animal nosed
it several times but did not seize it.   When moved with the
probe, it was taken and swallowed.   A piece of meat was then
refused.

A study of the behavior exhibited in this experiment reveals
a number of reactions which were found to be characteristic
of other individuals under appropriate stimulation.   First, there
is an approaching or following reaction.   The hungry animal
approaches a motionless object, or follows one moved in front
of it.   Secondly, there occurs a nosing reaction, which consists
of placing the anterior end of the snout, where the external
nares are situated, on the object under investigation, where it
may be held for several seconds.   This reaction is strongly sug-
gestive of "smelling," and is one of the most striking occur-
rences in the feeding behavior of the newt.   Thirdly, the object
may be seized or snapped at, and lastly, if taken into the mouth,
it may be swallowed.   The problem lay in determining whether
any one of these reactions is initiated by a stimulation of the
olfactory receptors.

The approaching reaction.   The approaching reaction was
first studied.   The importance of sight in this response was
easily demonstrated.   If a small piece of meat on the end of
a wire was moved about in the water four or five centimeters
in front of an animal, it was eagerly pursued.   When one ap-
proached the meat, others usually followed, until all the occu-

pants of the aquarium nearby became alert or active. If, next, a roll of filter paper was substituted for the meat, it, in turn, was followed in the same way, and the response to the inedible object was just as marked when the meat was not introduced at all; in fact, paper moved along the outer surface of the glass aquarium was watched and followed.

Finally, an experiment was devised to test reactions to a stationary object, and to show whether meat would be found more quickly than something from which no material capable of producing chemical stimulation could possibly emanate. A piece of raw beef was hooked on to the end of a wire fastened into a wooden bar, which was wedged between the sides of the aquarium above the surface of the water. In this way the meat was held in a fixed position in the water a few millimeters above the bottom of the aquarium, in which were placed five newts. The time elapsing between the introduction of the meat and its discovery by one of the animals was recorded. Care was taken that the animals should not see the meat as it was being placed in position, and thus be attracted by its movement. When the bait was discovered, nosed and snapped at, or seized, it was removed before it could be eaten, and in no two consecutive trials was it placed in the same position in the aquarium. In five trials, the average time taken to discover the meat was 1.8 minutes. Five trials were then made with the substitution of a ball of filter paper for the meat, when the average time taken for its discovery was 3.3 minutes. Upon repeating the experiment, the results were reversed. The average time taken to find the meat was 2.4 minutes, whereas the filter paper was located in 1.2 minutes. In the ten trials, the difference in the average times taken to find meat and filter paper was not more than a few seconds.

All these tests, and subsequent ones, indicate that the approach to an object, edible or inedible, is a visual reaction, and that, under the conditions described, if smell plays a part in food recognition, it does so after the animal has discovered and moved to the source of the stimulus.

The seizing reaction. In the reactions to the stationary meat and filter paper one significant difference was noted. Whereas the meat was always nosed and seized, or snapped at, the filter paper, although invariably nosed, was bitten only five times in

the ten trials. In the first experiment with cotton, plain and soaked in meat juice, when there was practically no difference in the appearance of the two pieces offered, similar results were obtained. In both experiments, however, discrimination between the inedible and edible objects (if cotton soaked in beef juice may be termed edible) was not perfect. The plain cotton was taken twice, and the filter paper snapped at five times. Other things, therefore, besides chemical stimulation may call forth the seizing reaction.

When the object, with which the test is being made, is fastened to the end of a probe, and is offered in that way to the animal, the movement of it becomes a possible factor in determining the response. Accordingly, the effect of motion of the proffered object was next investigated. A ball of filter paper, hooked to the end of a wire, was held firmly in position beneath the water by the method already described. A newt was then allowed to wander about the aquarium until it approached, nosed and deserted the filter paper. The paper was then either fastened to a probe and moved about near the animal, or it was rolled over the sand on the bottom of the aquarium. Several tests were made, involving three individuals. In three cases the movement of the filter paper induced the seizing reaction. One animal snapped it from the end of the probe four times in succession, and the other two not only seized but swallowed it. An inedible object in motion, therefore, may be taken into the mouth or even swallowed, whereas the same thing stationary is nosed and rejected. An explanation of this behavior is offered on a succeeding page.

Finally, as noted above, a fixed piece of filter paper is sometimes seized. Several factors may be influential in exciting this reaction, but the most important one, I believe, is hunger. An animal, which undoubtedly is very hungry, may cease temporarily to use its powers of discrimination, and seize and swallow filter paper almost as readily as meat, even when the former is not in motion. When, however, such an animal is fed, a different reaction may be obtained. The filter paper ball is then approached and nosed, but not seized. The following tests serve to illustrate the effect of both hunger and a moving object on the newt's feeding behavior. An animal took several pieces of filter paper from a wire in a fixed position. One or

two of these were swallowed. It was then fed with meat, after which it nosed, but refused to snap at stationary filter paper. The paper was next moved about in the water, when it was actively followed and seized.

From the experiments described above, it may be seen that, in order to test satisfactorily the relation between chemical stimulation and the seizing reaction, several factors must be eliminated. The desired results were obtained in the following way. Five animals, isolated in an aquarium, were carefully fed, so as to prevent any danger of excessive hunger. Two wires were fastened to a wooden bar so that their free ends reached nearly to the bottom of the aquarium when the bar was laid across the top. Two cheese cloth bags, 9 to 12 millimeters in diameter, were next made, one of which was filled with meat, and the other with cheese cloth. The bags were then tied to the ends of the wires, and the cross bar placed in position. By this method, two bags of approximately the same size and appearance, were held about 33 centimeters apart, a few millimeters above the bottom of the aquarium. The reactions of the newts to the bags were then watched for a half hour, the positions of the two being exchanged at the end of fifteen minutes. The result of this experiment was as follows. The bag containing meat was approached and nosed about 29 times, and bitten as many as 85 times. Since, frequently, three or four newts were snapping at the bag at once, an accurate record was difficult to obtain. Reactions to the cheese cloth bag were quite different. It was approached and nosed 17 times, but no attempt was made to seize it. As the bag was being lowered into position, it was snapped at by one of the animals, a response initiated by its movement. Three hours later, the experiment was repeated with similar results. The baited bag was approached and nosed 22 times, and bitten 94 times, whereas the other one was nosed 9 times and not once seized. In neither experiment was a case observed where an animal carefully nosed the baited bag and then failed to snap at it. These tests show conclusively that Diemyctylus is able to discriminate perfectly between two bags, one containing meat and the other not, and that the food sensing occurs after the bag is approached and before it is snapped at, or taken into the mouth.

The question next arose: Were the olfactory organs involved

in the reactions just described? To answer this question it became necessary, first, to ascertain in what way the stimulus reaches the receptors, and, secondly, after preventing any possibility of olfactory stimulation, to compare reactions then with those already recorded.

Certain intermittent mouth movements of Diemyctylus are conspicuous. These consist of a rather slow expansion of the floor of the mouth, followed by a sudden contraction, at which time the mouth is slightly opened. If carmine suspended in water is squirted from a pipette over the snout, it is drawn in through the external nares as this expansion progresses, and expelled from them, and from the mouth, when the contraction follows. Normally, therefore, any solution capable of producing olfactory stimulation flows through the nasal chambers, passes through the internal nares, and enters the mouth, and later a portion of it is expelled in a reverse direction by the same paths.

To prevent the flow of water through the olfactory chambers, the snout was first thoroughly dried, and then the external nares were covered with a thin layer of a celloidin preparation know commercially as "Cur-a-cut." The day after experimenting with the bags, the five animals tested were treated in this way. On the following morning one of them had lost the cap of celloidin, through shedding its skin, and another took no interest in meat which was offered it. The remaining three followed and snapped at meat, and exhibited normal behavior in every way. These three were tested for an hour with the two bags as before, the positions of the two being exchanged every fifteen minutes. The reactions to the bag containing meat were as follows. Animal A nosed it 3 times but did not bite it. B nosed it twice and left it both times. C nosed it 8 times and deserted it in every instance except the first, when it was snapped at about 10 times. The cheese cloth bag was nosed once by A, and twice by C. Five hours later the experiment was repeated, after all three had followed filter paper attached to the end of a probe. A nosed the cheese cloth bag once, B nosed it once and the baited bag 3 times, and C nosed each 4 times. Once C, after nosing the baited bag, snapped at it 8 or 9 times, but in all other cases there was no seizing reaction. Thus, in the 20 responses to the bag containing meat, the seizing reactions oc-

curred only twice, and an explanation of the exceptional behavior of C may probably be found in the following observation. Before the bag was bitten in the second experiment, the animal nosed it, and then, directing its snout downward, expelled water from the mouth; a fact noticed by the movement of the sand on the bottom of the aquarium. It then turned to the bag and attempted to seize it. Tests with carmine showed that an animal with its nostrils covered draws in and expels a small amount of water through the mouth. In view of these and subsequent observations, it seems quite likely, therefore, that in the two instances recorded material emanating from the meat was taken into the mouth in considerable quantity, and reaching the nasal chambers by way of the internal nares, stimulated the olfactory receptors.

The celloidin caps were removed after the experiment last described, and on the following morning the three newts were tested for an hour as previously. Both bags were nosed several times by B but neither was bitten. A, on one occasion, snapped at the baited bag after nosing it, and another time failed to do so. The cheese cloth bag was nosed but not seized. C nosed the baited bag carefully 4 times, and snapped at it in each instance. Once a hasty nosing of the bag was not followed by the biting reaction. This experiment was rendered somewhat unsatisfactory on account of A and C shedding their skins, an operation which always interferes with feeding. Five hours later, when the skins had been cast and the nasal organs given a longer time for recovery from the effects of non-use, the animals were again tested for an hour. The reactions of all were much the same so they need not be described individually. The cheese cloth bag which was nosed 21 times was not bitten once, whereas the baited bag, nosed 17 times, was snapped at 56 times. In but a single instance was the nosing of the bag containing meat unsucceeded by the seizing reaction (when the response was a nosing of the sand beneath the bag); in short, the newts had regained their normal ability to sense concealed food.

Results in accord with those set forth above were obtained by another method. As Reese showed, Diemyctylus usually responds to an extract of raw beef by snapping at it directly or at the sand upon which it settles. By means of a pipette

some meat juice, prepared by the method already mentioned, was squirted over the nostrils of a newt in such a way that the animal could not see the pipette. This was done ten times, and each time the response was a snapping of the jaws. Ten trials with water alone caused no reaction. At the conclusion of these tests the external nares were covered with "Cur-a-cut." Three quarters of an hour later the animal snapped at meat offered it on a probe, followed it about the aquarium, and in no way gave evidence that the presence of the celloidin cap was disturbing. It was then tested ten times with meat juice which called forth no response. The tests were repeated over an hour later with similar results: the snapping reaction failed to occur, although the animal followed and bit at filter paper in a normal way. The "Cur-a-cut" was next removed, and after 15 minutes had elapsed, 10 tests were made with meat juice. A positive response occurred four times. Twice the juice was snapped at, once the sand, and once the sand was nosed. An hour and a half later the reactions to the extract were the same as in the first tests of the experiment, viz., 10 trials resulted in 10 snapping responses. Another individual gave a series of reactions differing only in detail from the last. Four hours and a half elapsed after the nostrils were covered before the animal responded normally to filter paper and meat. Twenty tests with meat juice then failed to induce the usual snapping reaction. Five hours after the "Cur-a-cut" was removed, it was tested with the juice, when it responded six or seven times in 10 trials. A third animal reacted to the meat extract somewhat erratically on the first and second day after the nostrils were covered. Upon examination it was found that the "Cur-a-cut" had loosened so that one nostril was practically uncovered.

From the results obtained in these two types of experiments, one may fairly conclude that the usual snapping at beef extract, or at a bag containing meat, is a reaction initiated by a stimulation of the olfactory receptors, and that when an object is nosed, it, in truth, is being tested by the sense of smell. There is, however, another possible interpretation of this behavior, although one not at all probable. It is conceivable that the stimulating materials may pass through the nasal chambers and internal nares and affect the gustatory receptors of the mouth, and that the failure of the animal to respond

when the external nares are covered is really due to the lack of stimulation of the oral receptors, or perhaps to an insufficient stimulation of them, for, as already stated, a certain amount of water unquestionably is taken into the mouth when the nares are sealed.

In order to determine conclusively which interpretation of results was the correct one it became necessary to sever the olfactory nerves, an operation accomplished with little difficulty. A small opening was made in the roof of the cranium above each nerve, a fine pointed scalpel was inserted, and the cuts made. Notes made on the behavior of a newt with its peripheral olfactory apparatus rendered inoperative in this manner are as follows. Before the operation, which was performed at 10 A. M. on July 24, it snapped at meat, filter paper and meat juice. 10:13 A. M.—The animal showed no ill effects from the operation whatsoever. It followed and snapped at meat, and pursued a ball of filter paper rolled over the sand, a characteristic response of the normal individual. Meat juice, however, induced no reaction in five trials. A piece of meat was then immediately seized and swallowed. 10:30 A. M.—Meat was pursued and snapped at as before, but in five trials with meat juice no reaction appeared. It then followed meat moved through the sand, when the juice again brought forth no response in five trials. 11:15 A. M.—By squirting a mixture of carmine and water over the olfactory apertures it was clearly demonstrated that the operation had in no way interfered with the normal flow of water through the nasal chambers and the mouth. July 25, 8:30 A. M.—The newt followed a wad of filter paper in characteristic manner. 9:50 A. M.—Several tests were made with meat juice without response. A piece of meat was actively followed before, between and after the tests with beef juice. 3:50 P. M.—A bag filled with cheese cloth was nosed as normally. Then one containing meat was substituted for the first, and the animal induced to approach by moving it. It was nosed for many seconds and then deserted. (Another animal with functioning olfactory organs nosed the same bag and snapped at it actively.) A roll of filter paper was immediately pursued and seized, when it was taken away and the animal fed with meat.

The behavior of two other individuals whose olfactory nerves

· were cut need not be reported in detail. The day after the operations both took meat from a probe and followed and snapped at filter paper. If there were any general ill effects from the operations they could not be detected through any modification of behavior. Tests with carmine indicated that the flow of water through the nasal organs was normal. Both failed absolutely to respond to meat juice squirted over the olfactory apertures, although before the nerves were cut their reactions to it were very pronounced. The effect of a moving object on the behavior of an animal deprived of the sense of smell was most striking. In one instance it was only with great difficulty that the seizing reaction could be induced, for the newt persisted in its attempts to test the edibility of the meat by smell. It was nosed constantly on being moved through the sand, but not taken into the mouth. Finally, after continued agitation, it was seized and swallowed.

The results of the experiments last described indicate that the olfactory receptors, and not the gustatory ones, are those stimulated by substances in dilute solution such as meat juice. When the stimulus is prevented from reaching the former, or when their connections with the brain are severed, the results are the same, viz., the seizing or snapping reaction does not take place, provided, of course, it is not induced by a stimulus of quite a different character. I conclude, therefore, that Diemyctylus reacts to olfactory stimuli, and that the sense of smell plays an important part in food recognition.

The fact that a newt often seizes an inedible object such as filter paper only when it is in motion demands some explanation. In many cases this reaction probably occurs because the motion of the object interferes with a satisfactory nosing of it, and accordingly it is taken into the mouth where it may be tested by taste. An animal following and attempting to scent a moving piece of cotton or filter paper was of frequent occurrence, and very often the seizing reaction followed. In other instances, however, there appeared to be no attempt on the part of the animal to test the edibility of the object by the sense of smell, for it was immediately pursued and secured. An explanation of this behavior, I believe, is to be found in the character of the natural food of the animal. An examination was made of the stomach contents of a dozen newts which

were collected in the early part of August. Admitting of identi-·
fication were four snails of two genera, one water-boatman
(Corisa), one caddis-worm, several midge larvae (Chironomidae)
and three amphipod crustaceans. Since Diemyctylus feeds
upon such actively moving organisms as crustaceans and cer-
tain insects it must in many instances have no time to use its
olfactory organs, but would depend wholly on its powers of
vision and quickness of action in securing its prey; and in
consequence of such experience in nature it might be expected
to snap at a bit of moving filter paper in the aquarium. On
the other hand, the presence of insect larvae concealed in their
cases, or snails within their shells, may possibly have been
recognized by the sense of smell.

REESE'S EXPERIMENTS

Some of the work of Reese on the reactions of Diemyctylus
to chemical stimuli, together with certain conclusion, may be
briefly reviewed. Reese records the results of experiments
planned to show whether sight or the telaesthetic sense is the
one used by the newt in finding food. The animals were first
tested by comparing their reactions to pieces of meat with those
to inedible objects such as cloth, cotton and filter paper held
in forceps. Secondly, the effect of meat juice squirted over the
snout was studied.

In testing the animals by the first method the motion factor
enters, a thing which evidently the author did not attempt to
control. On page 191 he writes: "It would follow small taste-
less objects of various colors and would often seize them, but
usually disgorged them immediately," and after experimenting
with meat juice squirted over the nostrils concludes: "In secur-
ing food, then, it is probable that Diemyctylus uses both sight
and the telaesthetic sense, perhaps the latter more than the
former." Unquestionably both sight and smell are used in
obtaining food, and I believe I have shown the part played by
each. The seizing reaction undoubtedly was called forth in
many instances not so much by sight of the object as by sight
of it *in motion*. If the animals had been tested with stationary
objects by methods such as I have described, their marked
ability to discriminate perfectly between the edible and inedible
prior to seizure would in all probability have been demonstrated.

The reactions I obtained by squirting meat juice over the nostrils were like those reported by Reese.

After describing the reactions of Diemyctylus to "liquid chemicals," Reese attempts to distinguish between the sense of smell and taste. The time during which the feeding response is inhibited after cocaine is applied to the external nares is compared with similar inhibition occurring after temporarily placing cotton soaked in cocaine within the animal's mouth. The results obtained are not convincing, for, as the author points out, they are "somewhat conflicting" and open to several interpretations.

As a final test, the olfactory nerves were cut. The method is described as follows: "It was found by dissecting preserved specimens that, by inserting the points of a fine pair of scissors into the two posterior nares, and cutting the intervening tissues, both olfactory nerves could be sectioned with one quick cut. With the four selected animals this was done, after administering just enough ether to keep them from struggling." Reese's experiments upon the three animals which survived the operation and his conclusions are as follows. "These three recovered from the ether in a few minutes and the morning after the operation they were as active as ever, and gave no indication of being any the worse for the operation. Once or twice a day for more than a week they were tested with a bit of raw meat, but in no case attempted to seize it. Two of the animals paid no attention whatever to the meat, while the third, on two or three occasions, followed the meat (and also a piece of filter paper) without snapping at it. Juice from raw meat and from earthworms, described above caused no reaction whatever, though samples of both caused the snapping response in normal animals.

"After having been without food for about two weeks the animals, stimulated by extreme hunger, began to snap at meat or filter paper that was moved near them. If permitted to do so they would swallow the filter paper as readily as the meat. They would not seize either meat or paper unless it was in motion.

"While it is hard to understand why, if sight be the sense used, cutting the olfactory nerves should make an animal less apt to *follow* a bit of meat or a tasteless piece of paper, the

absolute refusal of these animals to eat, after severance of the olfactory nerves, seems to show that the olfactory sense is the one mainly used by Diemyctylus in recognizing food.".

The behavior of these animals does not justify, to my mind, the author's conclusion. The nearly complete disappearance of the following reaction, and "the absolute refusal of these animals to eat" seems to show little else than a general physiological disturbance following the operations. Of the three newts, whose olfactory nerves I severed, one followed and snapped at meat in a few minutes after the operation, and the other two did the same on the day succeeding. Such reactions only showed that the animals after the operations were behaving in respect to a *moving* object as they had before, thus giving evidence that they were, in general, physiologically normal, and accordingly in suitable condition for experimental study by the methods already described. Judging from the behavior of my animals, it seems certain, therefore, that those operated upon by Reese really did give evidence of being "the worse for the operation," and accordingly their failure to respond to juice from meat and earthworms might have been attributed to causes other than non-functioning olfactory organs. My method of operating was quite unlike that of Reese, a fact explaining, in all probability, the differences in behavior described.

SUMMARY

1. An inedible object, such as a ball of filter paper, suspended in an aquarium is discovered, approached and nosed by Diemyctylus as quickly as a piece of meat.

2. A cheese cloth bag containing meat is approached, nosed and snapped at, whereas a similar one filled with cheese cloth is approached and nosed but no attempt is made to seize it.

3. When an extract of raw beef is squirted over the external nares, the newt responds by snapping its jaws or biting at the sand on the bottom of the aquarium where the juice settles.

4. When the peripheral olfactory apparatus is rendered inoperative, both bags are approached and nosed but neither is seized, and beef extract squirted over the snout excites no reaction.

5. A moving inedible object may be seized or even swallowed, whereas the same thing stationary is nosed and rejected.

CONCLUSIONS

1. The approach to an object, such as cotton, filter paper or meat, is a visual response.

2. When the object is nosed its edibility is being tested by the sense of smell.

3. Snapping at beef juice and stationary edible objects are reactions dependent on stimulation of the olfactory receptors by substances in dilute solution.

4. The seizure of a moving inedible object is a reaction probably correlated with the character of the natural food of the newt. In all likelihood sight is the sense used by Diemyctylus in the capture of actively moving organisms, whereas other food located through vision is often recognized as such by the sense of smell.

REFERENCES

BAGLIONI, S.   Contributions expérimentales à la physiologie du sens olfactif et
    1909.   du sens tactile des animaux marins.   Archiv. Ital. de Biol., T. 52,
                pp. 225–230.
COPELAND, M.   The olfactory reactions of the puffer or swellfish, Spheroides macu-
    1912.   latus (Bloch and Schneider).   Jour. Exp. Zoöl., vol. 12, pp. 363–368.
PARKER, G. H.   Olfactory reactions in fishes.   Jour. Exp. Zoöl., vol. 8, pp. 535–
    1910.   542.
    1911.   The olfactory reactions of the common killifish, Fundulus hetero-
                clitus (Linn.).   Jour. Exp. Zoöl., vol. 10, pp. 1–5.
REESE, A. M.   Food and chemical reactions of the spotted newt, Diemyctylus
    1912.   viridescens.   Jour. An. Behavior, vol. 2, pp. 190–208.
SHELDON, R. E.   The sense of smell in Selachians.   Jour. Exp. Zoöl., vol. 10,
    1911.   pp. 51–62.

MATURATION AND USE IN THE DEVELOPMENT OF AN INSTINCT

J. F. SHEPARD AND F. S. BREED

From the Psychological Laboratory, University of Michigan

Two figures

INTRODUCTION

The work reported in this paper was done in the Psychological Laboratory of the University of Michigan during June, July and August, 1912. The problem grew in a very natural way out of a previous study[1] of the pecking instinct in barred Plymouth Rock chicks. In this earlier work a method was devised whereby the course of development in accuracy of the pecking reaction was satisfactorily traced. After the developmental curve of the instinct had been found, the question arose as to how much of the improvement from day to day is attributable to practice and how much is due to maturation apart from practice. To quote from an earlier article:

"One sometimes speaks of the *modifiability* of an instinctive action like that of pecking, but wherever this term has been employed in this paper in connection with instinct no more has been mplied than the objective fact of improvement in accuracy. an increasingly successful adjustment of parts in a more comprehensive function. The problem still remains, Is this development dependent upon practice, or is it the natural functional correlate of structural maturation independent of practice? Swallows are reported to be able to fly without previous practice. If the pecking of chicks could be successfully inhibited for a week's time without doing violence to the normal physical condition of the animals, would the accuracy of the reactions at the end of that time average 36.67 on a scale of 50, the average for our lot of twenty-one? There is evidence in support of the belief that such chicks would very quickly be pecking with average efficiency, without anything like the

---

[1] F. S. Breed. The development of certain instincts and habits in chicks. *Behavior Monographs*, 1911, vol. 1, no. 1, p. 14 ff.

amount of practice chicks would have had by this time when growing naturally. In other words, mprovement does not depend entirely upon practice. How much of the improvement does depend upon practice, * * * So far as the facts are concerned, the most one can say is that the development of the pecking instinct proceeds somewhat without practice and is hastened by it. Maturation and use run along in time together. No means has yet been devised of measuring the amount either factor apart from the other contributes to the development of the pecking reaction." [2]

PROBLEM AND METHOD

To devise and apply some method of separating these two factors became the problem in the experimentation we are reporting. The same variety of chicks was used as in the earlier experiments. The same make and style of incubator and brooder were also employed. As before, Cypher's Chick Food was used in the tests. The method of recording reactions and measuring accuracy was exactly the same as in the previous work. The terms striking, seizing, and swallowing denote here as there three distinguishable aspects of the chicks' feeding response, the term missing denoting failure to hit the object. As they appear in our records, the above terms have the following definite meanings: (1) Missing denotes all cases of the pecking reaction in which the bill failed to hit the particular object supplied by the experimenter; (2) striking, those cases in which the bill hit the object without seizing it; (3) seizing, cases in which the object was grasped momentarily in the bill and then dropped (not rejected); and (4) swallowing denotes what may be termed the perfect or complete reaction, the object being struck, seized, and swallowed in an errorless series or chain of movements. To facilitate the taking of records, the Arabic numerals 1, 2, 3, and 4 were employed to represent missed, struck, seized, and swallowed, respectively. Note was taken, of course, of the reactions independently of the number of food particles pecked at, for a single grain sometimes called forth a half dozen or more reactions in succession.

So much then for this study as it is related to certain previous work on the same instinct. Now a word in regard to

[2] Loc. cit., p. 40.

the method devised to test the effect of maturation apart from practice. The feeding reaction in its first intent being a response to an optical stimulus, it was thought feasible to prevent practice by keeping the animals in darkness prior to their first tests. To protect the chicks from light from the first, the incubator door was opaquely sealed before the date of hatching, and when the hatch was considered finished the animals were removed from the incubator to a dark-box during the night while the single window in the incubator room was shaded as a further precaution. The dark-box was lined with dull black cotton cloth and covered with the same material. In this box the chicks were transferred to a dark-room and kept therein, under a dark-curtained indoor brooder which had been made ready in advance. This brooder was heated by a system of galvanized sheet iron pipes which led from an oil lamp outside the dark-room to the brooder radiator and thence returned to the outside. No light from the heating apparatus was evident in the dark-room. The room in which the chicks were thus kept was entered through an adjoining dark-room so that light might not be admitted with the going and coming of the experimenters. The dark-room conditions having been satisfactorily arranged, a greater difficulty was confronted—that of artificially feeding the animals during the period of dark-room confinement. It was soon found futile and seemingly unnecessary to attempt feeding during the first twenty-four hours of this period. The chicks, as a rule, did not react positively to food on the first day. On the second day of the period, however, they usually began to take active part in the operation and made the attempt at feeding a much more successful one. The food in this case consisted of the regulation chick food, corn meal, and bread crumbs, all slightly moist. The chicks were taken from the dark-box one at a time, the body of an animal was clasped over the back in the hand of the experimenter, the bill was held open between the thumb and forefinger of this hand, and the food inserted in the mouth by the hand that was free. The chicks, when not taken too early, readily swallowed food thus administered. The amount supplied was regulated by the felt protrusion of the crops. Water was administered by a pipette gently introduced into their mouths. In this manner the chicks were fed and watered in the dark-room twice daily. The time

required for feeding was about 15 minutes per individual. It is worthy of remark here that, inasmuch as the death rate of the chicks was later found to increase with the length of the period of confinement, there seemed to be either a defect in our technique or a natural limit to this method of preventing practice.

FIRST REACTIONS IN THE LIGHT

When brought to the experiment table after their stay in the dark-room, the chicks generally stood quiet and inert for five minutes or more. The time recorded for one individual was ten minutes; for another, fourteen. To provide against possible difficulties of light adaptation under which the animals might be laboring, the members of group III were allowed to remain in the light from fifteen to thirty minutes before the first tests were undertaken. During this interval they were held by an assistant in order to prevent practice. The above control proved fortunate in view of a later observation made on the chicks of group V during their first few hours in the lighted experiment room. When placed in a dark-lined box, open at the top, half of which was shaded by the side of the box nearest an adjoining window, these chicks crowded into the shaded region. When moved repeatedly into the area of greater light intensity, they as often returned into the shade. Direct sunlight was excluded. Their phototropism had been reversed, at least temporarily, by the previous confinement in darkness, for chicks are known to be by nature positively phototropic. Coupling with this the further fact that the animals blinked noticeably on being first brought to the light, one may be inclined to conclude that the eyes of the animals were abnormally or pathologically affected during the first tests. However, even when special measures were not taken to adapt the chicks, the period of inactivity at the start gave considerable if not sufficient opportunity for adaptation. Furthermore, it is improbable that the normal accuracy of vision in these chicks was mpaired, for their first records, compared with those of the standard group, show even a smaller average number of "missing" reactions.

During this period of inactivity they devoured with apparent relish food that was inserted in their mouths, and even excitedly gave the food twitter when thus fed. But left to themselves

they soon lapsed into inactivity aga'n. A turning point in their behavior came when they succeeded in swallowing a grain after one of their more or less indifferent pecks. Energetic pecking thereupon ensued. The contrast between an animal's attitudes before and after swallowing a grain of its own pecking was very marked. Anthropomorphically speaking, one might well say the trouble with the animal was that it did not know what the food particles were or were for.
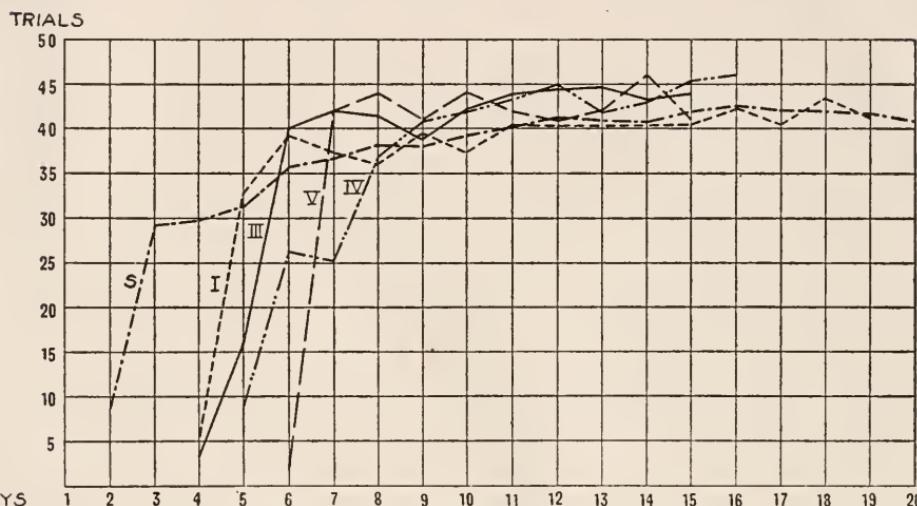
FIGURE 1.—Curves showing the course of development of the pecking instinct after artificial delay. S, standard curve, representing rate of improvement in accuracy under natural conditions. I, III, IV, and V, curves for corresponding groups of chicks in which the action of the instinct has been artificially prevented for three, three, four, and five days respectively, previous to the first tests. Data in table 1.

RESULTS OF PECKING TESTS

Two lots of chicks, divided into five groups, in all twenty-three in number, were tested. These groups were designated by the Roman numerals I, II, III, IV, and V. In figure 1 the corresponding curves for the several groups are designated by these same numerals. Each curve represents the course of development of the complete feeding coördination, that is, of reaction 4, for a given group. The number of perfect reactions in a series of fifty pecking reactions, the first fifty, on any given day, is assumed to be an index of the accuracy of the pecking

instinct on that day. For purposes of comparison we have reproduced as a standard a curve of development of reaction 4, plotted from the average daily records of twenty-one chicks (curve S, figure 1). Curve I is based on similar records of four animals whose practice in pecking was prevented, as above described, up to the beginning of their fourth day. The records of group II are not presented on account mainly of their incompleteness. Curve III shows the development of the instinct in a group of six chicks, also beginning their practice on the fourth day. In curve IV are represented averages for three chicks which were released from darkness at the beginning of the fifth day. There were six individuals in this group when the first records were taken. Of six chicks originally in group V, five died within three days after the first pecking records were taken. Curve V represents the records of the one animal that completed the tests. Practice was begun in this case on the sixth day. For data see table 1.

One of the most interesting features of the results is the very low initial records of all the chicks in which the action of the instinct was delayed. Who would have predicted that the greater maturation of groups I to V would not have enabled them to begin at a higher grade of efficiency than that of the standard group on the second day? As a matter of fact, all the chicks in the above groups began their pecking as the merest novices. Once we see the value for improvement of the first attempts, the fact that these records are in every case lower than the beginning records of the standard group may well be explained on the ground that the chicks of the standard group had twenty-four hours of freedom in the light prior to their first tests, whereas the other chicks were tested immediately upon being released from the dark-room.

The next point that seems to be of rather exceptional interest is the rapidity and amount of improvement during the first two days of practice. Within this time the dark-room chicks attained the level of accuracy normal to their age. Thenceforward the progress apparently assumed its natural course. It seems probable that the peculiar change in the shape of the standard curve at the beginning of the third day is not entirely a matter of chance. The rest of the curves are of the same general character,—a rapid advance with the first two days of

TABLE 1

Pecking Efficiency After Artificial Delay, Shown by the Number of Perfect Reactions in a Daily Series of Fifty Trials

Day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	No. of chicks
Standard group.		8.7	29.3	29.8	31.4	35.9	36.7	38.2	38.	39.2	40.1	41.2	40.7	40.6	41.6	42.6	42.1	41.9	41.6	40.8	21
Group I				5.5	32.8*	39.3	37.3	36.	39.5	37.3	40.5	40.3	40.3	40.5	40.5	42.5	40.5	43.5	41.3		4
Group III.....				3.1	16.	40.	42.	41.3	38.8	42.3	44.	44.5	44.7	43.3	44.						6
Group IV.....					8.7	26.3	25.3	36.7	40.7	42.	43.3	45.	41.7	43.	45.3	46.					3
Group V......						2.	42.	44.	41.	44.	42.	41.	42.	46.	41.						1

*An evening record; morning record unsuccessful.

practice, followed by a gradual and fairly steady improvement
thereafter.   It seems to the writers that a given amount of
practice, quite constant for the different groups, is necessary
to smooth the way for the operation of a native capacity whose
efficiency is largely a function of the age of the animal.   In
other words, it is our view that the second portion of the curves
is almost entirely a record of maturation.   If this be true, and
further experimentation can no doubt establish the truth or
falsity of this conjecture, there would seem now to be some
explanation for the negative results obtained in previous tests
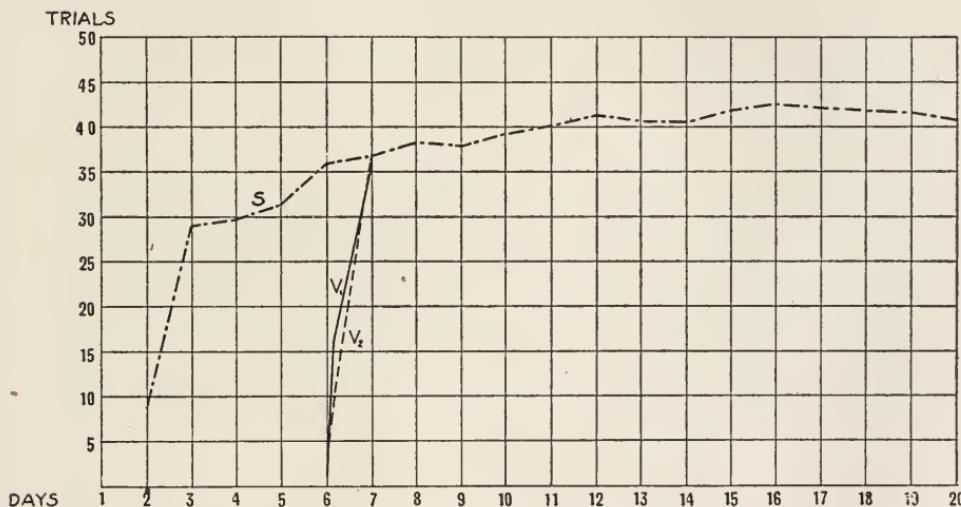
FIGURE 2.—Curves showing rate of improvement in accuracy of the pecking in-
stinct during the first twenty-four hours after five days' artificial delay. V_1,
curve for nos. 22 and 24; V_2, curve for nos. 23 and 27.   S, standard curve
reproduced for comparison.   Data in table 2.

of the effect of social influence on the development of this
instinct.

The effect of the first day's practice after an artificial delay
of five days from the time of hatching is indicated in curves
V_1 and V_2, figure 2.   The records first given show the degree of
accuracy in the first 50 trials—characteristically low.   It will be
noticed that as practice proceeded the improvement was both
rapid and regular.   Twenty-four hours from the time practice
was started the individuals of these two sub-groups reached an

average accuracy score of 36 and 37 respectively on the regular
scale of 50. The data are given in table 2.

TABLE 2

Rate of Improvement During the First Twenty-four Hours After
Five Days' Artificial Delay, Groups V_1 and V_2

Day.....................		6			7
Nos. 22 and 24, Group V_1	Time of test......	9:58 A.M.	10:31 A. M.	1:00 P. M.	10:15 A. M.
	Perfect reactions in 50 trials........	1.	8.5	16.	36.
Nos. 23 and 27, Group V_2	Time of test......	10:45 A.M.	11:21 A.M.	1:00 P. M.	10:15 A. M.
	Perfect reactions in 50 trials........	3.5	6.5	11.	37.

A critic may interpose at this point that the chicks, upon
being given their natural freedom after the first tests, improved
as they did because they made up lost practice in excessive
pecking. Careful observation of the animals did not attest this
view. Furthermore, there are two valid objections to this
objection: (1) Practice was necessarily limited by the food
allowance, and (2) practice was also limited by the food capac-
ity of the animals.

An answer to one more possible objection. One of the writers
found in previous experiments that chicks peck at and eat food
when light is excluded. On the basis of this fact it may be sup-
posed that dark-room conditions do not prevent the pecking
response and therefore practice. It should be noted, however,
that, in the earlier experiments referred to, all the animals had
practiced previously in the light. No evidence of pecking was
found while groups I to V were in the dark-room. These chicks
did not even peck for food while being artificially fed.

CRITICISM OF SPALDING

The accuracy of the first pecking reactions after artificial
delay has surely been much exaggerated by Spalding. It will
be recalled that Spalding employed a hooding device to prevent
practice for from one to three days. The hooding was intended
to permit the chicks to acquire enough control over their mus-

cles to enable them to give evidence of their instinctive power. If Spalding's device securely protected the eyes of his chicks from the light, which was apparently not true in all cases, we are inclined to believe that the first attempts of those animals would have been found upon careful study little if any more accurate than the efforts of his day-old chicks.

We are forced to conclude that another observation of Spalding has been too freely generalized. In his original article appears the following:

"Something more curious, and of a different kind, came to light in the case of three chickens that I had kept hooded until nearly four days old—a longer time than any I have yet spoken of. Each of these on being unhooded evinced the greatest terror of me, dashing off in the opposite direction whenever I sought to approach it. The table on which they were unhooded stood before a window, and each in its turn beat against the glass like a wild bird. One of them darted behind some books, and squeezing itself into a corner, remained cowering for a length of time. We might guess at the meaning of this strange and exceptional wildness; but the odd fact is enough for my present purpose. Whatever might have been the meaning of this marked change in their mental constitution—had they been unhooded on the previous day they would have run to me instead of from me—it could not have been the effect of experience; it must have resulted wholly from changes in their own organization." [3]

James, after quoting the above passage, does not hesitate, as Spalding does, to supply the meaning of "this strange and exceptional wildness:"

"Their case was precisely analogous to that of the Adirondack calves (of which James had been told by farmers in the Adirondack wilderness). The two opposite instincts relative to the same object ripen in succession. If the first one engenders a habit, that habit will inhibit the application of the second instinct to that object. All animals are tame during the earliest phase of their infancy. Habits formed then limit the effects of whatever instincts of wildness may later be evolved." [4]

[3] D. A. Spalding. Instinct. With original observations on young animals. *Macmillan's Magazine*, 1873, p. 289.
[4] William James. Principles of Psychology, vol. II, p. 397.

In the course of our observations chicks were taken from the dark-room and brought to the experiment table at the beginning of the fourth, fifth, and sixth days, as previously detailed. The pecking tests were conducted directly before a window, the animals working at a distance of about two feet from the glass. True these chicks had not been hooded. But in no case was an animal observed to run at the approach of the experimenter or show more excessive signs of fear. Generalization on the basis of these facts reported by Spalding seems highly premature.

SUMMARY AND CONCLUSIONS

In a previous study of the pecking instinct of barred Plymouth Rock chicks data were gathered from which a curve of development of the instinct was plotted. This curve represents the improvement in accuracy of the pecking coördination from the second to the twenty-fifth day. With this curve as a standard an attempt was made to determine the relative amounts contributed by maturation and use to this improvement. Two lots of chicks, divided into five groups, in all twenty-three in number, were tested. By confinement in a dark-room prior to the first tests practice was prevented for a definite time in each group—three, four, or five days from date of hatching. Meanwhile the animals were fed and watered artificially. The most interesting features of the results are (1) the uniformly poor initial records, and (2) the rapidity with which normal accuracy was attained. Regardless of the duration of the period of confinement, within the limits specified, the chicks began below an efficiency of 18% and with from one to two days' practice reached normal efficiency. In the first two days of the curves the necessary practice component, it seems, is represented, and in the remainder a record mainly of maturation.

The improvement ensuing upon the first practice was both rapid and regular. The rapidity was not due to excessive practice following the enforced delay of the instinct. If, as suggested, the curve after the first two days is mainly a record of maturation, there would seem to be some explanation for the negative results in previous tests of the effect of social influence on the development of this instinct.

Although chicks with previous practice have been found to

eat in the dark, these chicks were not observed to peck during the period of dark-room confinement.

Shortly after being brought to the light, chicks that had been in the dark-room five days were found to be negatively phototropic, at least temporarily.

Spalding has exaggerated the accuracy of pecking after artificial delay. The manifestations of fear after four days in darkness, as reported by Spalding, were not observed in these chicks.

THE HEREDITY OF SAVAGENESS AND WILDNESS IN RATS

ROBERT M. YERKES

Harvard University

In 1910 Professor William E. Castle suggested to me the desirability of studying the heritability of savageness and wildness in certain strains of rats which were being bred for studies in the heredity of structural characteristics at the Bussey Institution. I undertook the proposed investigation, and by the generous aid of Professor Castle and Doctor John C. Phillips I have been enabled to test the behavior of nearly three hundred individuals. The investigation is incomplete, and in this paper I propose to present merely a preliminary report, reserving the detailed account of my work, with the experimental data, for a paper to be published later, in some journal of genetics.

At the outset I made a preliminary analysis of the behavior of some of the rats in order to discover several traits which seemed to be fairly isolable and capable of reasonably accurate measurement. As a result of these observations, I decided to make tests of the savageness, wildness, and timidity of wild rats, tame rats, and of the first and second generation hybrids.

Preliminary attempts at measurement indicated that six grades, with respect to these several traits, might be utilized. These grades I designated as 0, 1, 2, 3, 4, and 5. The grade 0 indicates the absence of the various signs of savageness, wildness, or timidity. The grade 5 indicates the presence of these signs in maximal number and intensity.

In order to obtain a rough measure of the reliability of my judgments, I tested the individuals of several litters of rats with respect to the three traits designated and, later, without knowledge of my previous results, retested the same individuals. A comparison of the measurements thus obtained indicated that they were often the same and seldom differed by more than a grade. The results given below are typical.

No. of rat	Date	Savageness	Wildness	Timidity
59♂	Jan. 10........................	4	4	3
	" 17........................	4	3	2
69♀	" 10........................	3	3	4
	" 17........................	2	3	4
63♀	" 10........................	3	3	4
	" 17........................	3	3	3

The preliminary analysis of the behavior of rats, and my measurements, convinced me that I might profitably undertake a systematic study of savageness, wildness, and timidity in wild, tame, and hybrid individuals. Of these three traits, or possibly I should say, combinations of traits, timidity is the most difficult to recognize and satisfactorily measure. It is indeed extremely doubtful whether it can with sufficient certainty be distinguished from wildness to render measurements significant. I have attempted, however, throughout the investigation, to measure it and I shall report the results along with those for the other traits.

My method of testing the rats was to place a cage containing individuals to be examined on a table in the center of an otherwise unoccupied room. I then removed an individual from the cage in order carefully to observe its behavior. This removal was effected by means of my gloved hand, when that method could safely be used, or, in the case of extremely savage animals, by means of a pair of placental forceps which were used to grasp the animal by the tail.

The chief indications of savageness noted and relied upon as a basis for grading are (1) biting; (2) exposing or gnashing the teeth; (3) jumping at hand or forceps; (4) squeaking.

Similarly, the chief indications of wildness are (1) attempts to hide from view in cage or in hand; (2) random and excited running about in the cage or excited attempts to escape from the hand or the forceps; (3) squeaking; (4) urination and defecation.

Timidity is indicated (1) by attempts to avoid the experimenter; (2) by a kind of chattering or gnashing of the teeth; (3) by cowering and what looks like trembling; (4) urination and defecation.

From my notes, I reproduce the following statements concerning these several traits of behavior. "Savageness is of two

kinds, defensive and offensive. Of each there are several indications. The former deserves a higher grade than the latter. Defensively savage individuals are likely to jump at the observer and cannot be safely handled even with the gloved hand. Offensively savage rats may safely be handled: it is necessary only to avoid hurting them. Wildness almost invariably accompanies savageness. Timidity may or may not. An extremely savage and wild rat may exhibit little fear of the experimenter. A savage and aggressive wild rat fights, whereas a timid rat cowers, trembles, and chatters."

The animals observed, numbering about three hundred (300), consisted of wild rats, tame rats, and first and second generation hybrids.

The wild rats were captured either in Belmont or in Cambridge, Massachusetts, and were, with one exception, adult males. Observations and tests on them, made in several instances immediately after capture and again after they had been in captivity for a year, indicated extreme savageness and wildness, with variable timidity. The grade of 5 for savageness was assigned to almost all of these individuals. In wildness, they were graded either 4 or 5, and in timidity 3, 4, or 5. As a result of their confinement in cages for a year, they exhibited a lower grade of wildness and timidity, but their savageness remained unchanged. It was impracticable and wholly unnecessary to repeat frequently the tests on these wild individuals.

The tame rats were taken from a strain in use for studies of coat color at the Bussey Institution. This strain has been bred in the Harvard Zoölogical Laboratory for at least ten years. A brief account of some recent experiments with these rats has been given by Professor Castle in a paper entitled "Some biological principles of animal breeding."[1]

As a result of certain experiments in selective breeding, two types of animal, each of which was used in my experiments are distinguishable in this strain. They are known as wide (W) and narrow (N) individuals. Both have black heads (hoods), but in the wide the black extends further back than in the narrow. The wide are known to have more wild blood than the narrow, and in these experiments they prove to be wilder and more savage.

---

[1] *American Breeders' Magazine*, 1912, vol. 3, no. 4.

Tests of savageness, wildness, and timidity were made with eight male and eighteen female tame rats (some wide, some narrow). Each individual was tested twice, the tests being separated by an interval of one month. In no case did the males receive a grade above o. All were so gentle and tame that they could readily be taken up in the ungloved hand and examined. The females were decidedly less gentle and tame than the males. Two of the eighteen tested received a grade of 1 for savageness and fourteen of the eighteen received a grade of 1 for wildness. The number receiving a grade above o for timidity was twelve.

The contrast between the wild and the tame rats with respect to savageness, wildness, and timidity is extremely marked.

The first generation of hybrids was obtained in almost all cases by crossing a wild male with a tame female. This mating is much more satisfactory, because more likely to yield offspring, than the mating of a wild female with a tame male. By crossing the first generation hybrids among themselves, without selection with respect to savageness, wildness, and timidity, the second generation hybrids were obtained. Up to the present, no third generation hybrids have been examined.

As the mating, numbering, and weaning of the rats used were attended to by Professor Castle and Doctor Phillips, the experimenter was wholly unprejudiced, while making his tests, by knowledge of the genetic relations of the individuals. Very rarely indeed did he know whether the individual under observation was a tame rat or a first or second generation hybrid rat. Thus, he was able to escape entirely the influence of possible presuppositions concerning the behavior of savageness, wildness, and timidity in heredity.

With a few exceptions, each individual was tested from three to five times, at intervals of several days. The first test was made, as a rule, at the age of about six weeks and the remaining tests usually covered a period of at least a month, sometimes two months. It was noted that in general the animals receive lower grades with repetitions of the tests. This is due in part to the experience of being handled, but even more to the fact that they become accustomed to seeing human beings and to being disturbed when fed or when the cages are cleaned. There is also some evidence that ageing has something to do with the change.

TABLE 1

RESULTS OF SUCCESSIVE TESTS OF FIRST GENERATION, F₁, (NARROW × WILD)
HYBRID RATS

Rat	Age	Date	Savageness	Wildness	Timidity
19♀	58 days	Sept. 25..................	5	4	4
		Oct. 2..................	4	4	3
		" 17..................	3	4	3
		" 24..................	1	2	2
20♀	58 days	Sept. 25...., ...	5	5	5
		Oct. 2..................	5	5	4
		" 17..................	5	5	4
		" 24..................	2	3	2
94♀	45 days	Aug. 7..................	1	1	1
		" 13..................	2	2	2
		Sept. 25..................	1	3	2
		Oct. 2..................	0	2	2
21♂	58 days	Sept. 25..................	5	5	5
		Oct. 2	4	4	3
		" 17..................	3	4	3
		" 24..................	2	3	2
22♂	58 days	Sept. 25..................	5	4	4
		Oct. 2..................	4	4	3
		" 17..................	2	3	2
		" 24..................	1	3	2
80♂	50 days	June 20..................	0	2	1
		July 5..................	1	2	1
		Aug. 7..................	0	1	1
		" 13..................	0	0	0

In tables 1 and 2 are presented, for contrast, typical results
obtained with groups of F₁ (first hybrid generation) males and
females and F₂ (second hybrid generation) males and females.

The individuals of these tables are all the offspring of crosses
between narrow tame rats and wild rats. The results indi-
cate (1) diminishing savageness, wildness, and timidity with
repetitions of the tests; (2) sex differences; (3) marked differ-
ences for the two generations. The F₁ individuals grade much
higher, on the average, in savageness, wildness, and timidity
than do the F₂ rats.

The results for seventy-eight F₁ individuals are summarized
in table 3. All of these individuals were the offspring of narrow
by wild crosses. The table presents, in the first horizontal line,
(a) the average age; (b) the range in age of the group; (c) the
average number of tests; (d) the range of tests; (e) the average

TABLE 2

RESULTS OF SUCCESSIVE TESTS OF SECOND GENERATION, F₂, (NARROW × WILD) HYBRID RATS

Rat	Age	Date	Savageness	Wildness	Timidity
52♀	75 days	Jan. 24	0	3	2
		" 31	0	1	1
		Mar. 11	0	0	0
		" 18	0	0	0
55♀	75 days	Jan. 24	0	0	1
		" 31	0	0	0
		Mar. 11	0	0	0
		" 18	0	0	0
64♀	80 days	Sept. 27	5	5	5
		Oct. 7	5	4	4
56♂	75 days	Jan. 24	0	3	2
		" 31	0	2	2
		Mar. 11	0	1	1
		" 18	0	1	1
53♂	75 days	Jan. 24	0	3	2
		" 31	0	3	3
		Mar. 11	0	3	1
		" 18	0	2	1
62♂	80 days	Sept. 27	5	5	5
		Oct. 7	5	5	4

grade attained in the first test for savageness; (f) in the last test for savageness; (g) the average grade for all tests (that is the average for the total number of tests given to the group). The same three values are given also for wildness and for timidity. Immediately below these averages appears the distribution of the rats in the grades 0 to 5.

In tables 3, 4, 5, and 6 the results for males and females are presented separately. Tables 3 and 4 present the results obtained from the offspring of narrow tame by wild crosses; and tables 5 and 6 those obtained from the offspring of wide tame by wild crosses.

It is apparent from table 3 that the F₁ narrow by wild individuals of both sexes grade high in savageness, wildness, and timidity. Without exception, the females grade higher than the males. Thus, the first test for savageness yielded the grade of 4.39 for the females and 3.45 for the males. This result is typical. The lower grades attained in the last test are noteworthy. If we designate the grade which is most frequent as

TABLE 3

Summary of Results for First Generation Hybrids, F_1 (Narrow × Wild)

	Age		No. of tests		Savageness			Wildness			Timidity		
	Av.	Range	Av.	Range	1st test	Last test	Av.	1st test	Last test	Av.	1st test	Last test	Last Av.
	42.45	25–91 da.	3.76	2–4	3.45	1.6	2.52	4.19	2.86	3.24	3.74	2.43	2.9
42 F₁ males	Distribution of rats in grades 0–5.			0	4	19	5	0	1	0	0	1	0
				1	6	3	8	0	4	1	2	9	3
				2	2	3	6	3	10	10	7	10	14
				3	2	10	9	6	12	11	6	15	9
				4	11	7	11	13	15	18	12	7	16
				5	17	0	3	20	0	2	15	0	0
	48.75	25–81 da.	3.67	1–4	4.39	2.5	3.31	4.44	3.22	3.78	4.19	2.64	3.33
36 F₁ females	Distribution of rats in grades 0–5.			0	0	7	0	0	0	0	0	0	0
				1	2	6	3	1	2	0	1	6	0
				2	0	5	7	0	10	3	3	13	10
				3	3	4	12	3	9	11	2	7	8
				4	8	8	12	10	8	13	12	8	14
				5	23	6	6	22	7	9	18	2	4

the modal grade, we have, in the case of the first tests for both males and females, 5 as the modal grade. In other words, this group of F_1 hybrids attain the maximal grade of savageness, wildness, and timidity with modal frequency.

Turning now to a comparison of the results of table 3 with those for the second generation hybrids as presented in table 4, we discover, first cf all, that the F_2 individuals, numbering one hundred and fifteen, grade very much lower on the average in savageness, wildness, and timidity than do the F_1 hybrids. A comparison of the results for the two sexes indicates a marked difference in that, whereas the F_1 females grade higher than the males, the F_2 males grade higher than the females. With respect to the distribution of individuals there is a great difference for the two generations, for whereas the F_1 individuals attain as their mode the grade of 5, the F_2 individuals in no instance attain a grade higher than 2 as the modal grade, and in most cases it is either 0 or 1. Thus, it may be noted in table

TABLE 4

SUMMARY OF RESULTS FOR SECOND GENERATION HYBRIDS, F_2 (NARROW × WILD)

	Age		No. of tests		Savageness			Wildness			Timidity		
	Av.	Range	Av.	Range	1st test	Last test	Av.	1st test	Last test	Av.	1st test	Last test	Av.
	50.76	21–112 da.	4.	1–7	1.37	.7	1.	2.37	1.83	2.04	1.91	1.46	1.63
46 F_2 males	Distribution of rats in grades 0–5.	0	24	34	27	0	6	2	1	8	2		
		1	7	5	7	12	17	15	17	22	24		
		2	2	1	5	16	12	17	20	7	13		
		3	4	2	2	11	4	6	4	6	3		
		4	5	1	2	3	4	3	1	2	4		
		5	4	3	3	4	3	3	3	1	0		
	46.87	21–112 da.	4.2	1–7	1.17	.49	.74	2.17	1.52	1.77	1.84	1.28	1.42
69 F_2 females	Distribution of rats in grades 0–5.	0	37	56	45	2	10	8	1	10	7		
		1	11	4	10	20	26	17	30	37	33		
		2	6	1	6	21	23	31	25	17	24		
		3	5	5	4	19	7	9	8	3	3		
		4	7	2	3	4	3	4	2	2	2		
		5	3	1	1	3	0	0	3	0	0		

4, that the modal grade for all of the averages under savageness is 0; under wildness or timidity, 1 or 2.

The results of tables 5 and 6 stand in striking contrast with those of tables 3 and 4. Although the numbers of individuals resulting from wide by wild crosses are small for both the first and the second generation hybrids, the differences which appear from comparison of tables 3 and 4 with 5 and 6 indicate clearly the influence of the wild blood in the wide tame parent.

We note from table 5 that fifteen F_1 individuals yield average grades which are about as high as those for the F_1 narrow by wild. There is slight difference, however, in the case of the F_1 wide by wild individuals for the sexes. The modal grade for savageness, wildness, and timidity is seldom below 4 for either males or females. In two cases it is 3.

The second generation of wide by wild individuals grades nearly as high as the first generation and is thus in marked contrast with the second generation of the narrow by wild

TABLE 5

Summary of Results for First Generation Hybrids, F₁ (Wide × Wild)

	Age		No. of tests		Savageness			Wildness			Timidity		
	Av.	Range	Av.	Range	1st test	Last test	Av.	1st test	Last test	Av.	1st test	Last test	Av.
	42	40–46 da.	3.44	1–5	3.78	2.78	3.44	4.44	3.11	3.78	4.		2.89 3.44
9 F₁ males	Distribution of rats in grades 0–5.	0	0	3	0	0	0	0	0	0	0		
		1	1	0	3	0	3	0	0	0	0		
		2	1	0	0	0	0	3	2	3	3		
		3	1	0	0	2	0	0	1	5	0		
		4	2	5	2	1	5	2	1	0	5		
		5	4	1	4	6	1	4	5	1	1		
	43	40–46 da.	4.00	3–5	4.	2.5	3.33	4.33	2.83	3.67	3.83	2.5	3.17
6 F₁ females	Distribution of rats in grades 0–5.	0	0	2	0	0	0	0	0	0	0		
		1	1	0	2	0	2	0	0	1	0		
		2	0	0	0	0	0	2	2	1	2		
		3	0	1	1	2	1	1	0	4	1		
		4	2	3	0	0	3	0	1	0	3		
		5	3	0	3	4	0	3	3	0	0		

rats. There is no very marked constant difference for the sex groups. The modal grade ranges from o to 4. It is most frequently either 2 or 3. This apparently indicates that savageness, wildness, and timidity are of lower grade development in the second generation than in the first generation of wide by wild individuals.

Finally, in table 7 are presented the results for the F₁ as contrasted with the F₂ narrow by wild hybrids, the sex groups having been combined. In this table, the averages for the first test alone are given. This test appears to be in all respects the most reliable measurement of the several traits. As appears, the first generation hybrids approximate the average grade of 4 in savageness, wildness, and timidity, whereas the second generation hybrids approximate the average grade of 2. The modal grade for the first generation individuals is 5 in the case of all three traits. For the second generation individuals it is o in the case of savageness and 2 in the cases of wildness and timidity.

TABLE 6
Summary of Results for Second Generation Hybrids, F_2 (Wide × Wild)

	Age		No. of tests		Savageness			Wildness			Timidity		
	Av.	Range	Av.	Range	1st test	Last test	Av.	1st test	Last test	Av.	1st test	Last test	Av.
	34.88	26–50 da.	3.18	1–4	3.06	1.82	2.24	3.71	3.29	3.35	3.18	2.71	2.65
17 F$_2$ males	Distribution of rats in grades 0–5.	0	2	6	2	0	0	0	0	0	0
		1	0	3	3	0	0	0	1	1	1
		2	2	2	6	1	3	2	4	7	6
		3	7	3	3	5	7	8	5	5	8
		4	3	0	1	9	6	6	5	4	2
		5	3	3	2	2	1	1	2	0	0
	40.09	26–50 da.	2.96	1–4	3.26	2.13	2.65	3.74	3.09	3.3	3.3	2.35	2.74
23 F$_2$ females	Distribution of rats in grades 0–5.	0	1	5	2	0	0	0	0	0	0
		1	3	3	2	0	1	0	1	4	1
		2	2	7	7	2	5	4	5	12	11
		3	4	2	5	6	12	11	6	4	6
		4	9	4	5	11	1	5	8	1	3
		5	4	2	2	4	4	3	3	2	2

TABLE 7
General Summary of Results for First and Second Generation Hybrids, (Narrow × Wild)

78 F$_1$ males and females		Savageness first test 3.92	Wildness first test 4.33	Timidity first test 3.97
Distribution of rats in grades 0–5.	0	4	0	0
	1	8	1	3
	2	2	3	10
	3	5	9	8
	4	19	23	24
	5	40	42	33

115 F$_2$ males and females		Savageness first test 1.27	Wildness first test 2.27	Timidity first test 1.88
Distribution of rats in grades 0–5.	0	61	2	2
	1	18	32	47
	2	8	37	45
	3	9	30	12
	4	12	7	3
	5	7	7	6

The results thus briefly presented in tabular form prove conclusively that savageness, wildness, and timidity are heritable behavior-complexes. It is hoped that the further study of these characteristics in the third generation hybrids, and in special matings from the first and second generation hybrids, may yield more definite results concerning the modes of transmission.

NOTES

NOTE ON THE SEX BEHAVIOR OF THE POITOU JACKS

RAYMOND PEARL

The practical live-stock breeder is in a position to make many interesting and important observations regarding the animals with which he works. What farmers and breeders have put on record furnishes practically the only basic data for the building of a comparative psychology of the larger domestic animals (*teste* the writings of Darwin, Romanes, Groos, and others). Unfortunately, however, the amount of such raw material for comparative psychological analysis and synthesis which has been made available to the trained psychologist by getting into the literary channels which are familiar or accessible to him, is only a small fraction of the total existing amount. The majority of farmers and stockmen are not prolific authors. Furthermore when their observations are published they are, in nearly every instance, printed in some agricultural paper, where they are most unlikely ever to come to the attention of the psychologist, and where they are at once practically lost for any purpose, owing to the ephemeral character of most such papers.

In view of these considerations I venture to call the attention of the readers of this journal to some observations which seem to me to be of a good deal of interest and value to the student of the comparative psychology of sex. These observations were recently reported in the Breeders' Gazette* (Chicago), by Mr. John Ashton, a European representative of the Gazette, and an accurate and well-informed writer on live-stock matters. The observations here recorded were made by Mr. Ashton during a visit to the famous mule-breeding district of France, Poitou. Here are bred mules of an especially valuable sort, and it was to study this mule breeding industry at first-hand that Mr. Ashton went there. In the course of a very interesting general

---

* Vol. LXIII, pp. 596-597, March 5, 1913.

account of the industry he describes the breeding behavior of the jacks in the following words:

"The jack farm has a large stone breeding barn having closely boarded boxes, in which the jacks are kept. These boxes have no windows and no openings, except a small space left between the ends of the boards and the ceiling for ventilating purposes, the result being that the animals are kept in total darkness. Each box is closed by a strong door, secured by a lock or bars and chains. At one end of the barn a peculiar yet simple arrangement to expedite breeding operations is constructed. Its general appearance resembles a pair of extremely heavy, long, narrow wagon shafts.   *   *   *

"After the mare is placed, with her head to the wall, between these shafts, the manure and straw lying on the ground in her rear are heaped up, or scraped away, in conformity with the size of the mare or jack. The close hitching of the mare to the cross-piece, together with the narrow width of the shafts, does not allow her to move about. If she shows any disposition to kick, hobbles are placed around her fetlocks. The tail is carefully arranged so as to keep it out of the way. Notwithstanding the great lascivity of the jack, he only demonstrates it in the presence of his natural female, and for this reason artificial means have to be introduced to prepare him for serving mares. These means vary somewhat in the different studs, but by far the most popular is that of singing a song known as the "trelandage," owing to it being composed of the monosyllables *tre* and *la*. This was the method of preparing the jacks on the first farm that I visited. At some haras the pronunciation of certain words in a peculiar tone seems to be in favor; at others a jerky whistling sound is practiced to achieve the desired object, while in some cases the simple act of clanging the door chains, turning the lock, or opening and closing the door several times causes the jack to manifest a keen desire. There are even some, but not many I am told, that do their duty at the first call, without any of these comical formalities.

"Sometimes it is found necessary to allow the jack to see a female of his own species, the latter being replaced by a mare at the proper moment. When this is done the mare is often draped so as to deceive the jack. Only the owners or the grooms in charge of the different jacks seem to understand the indi-

vidual weaknesses and predilections of their animals. It is notorious that many of the finest jacks are the most capricious. When every other means have failed, a young jack is placed near the mare, during which time his elder but less ardent brother is firmly held at a distance. This stratagem causes the latter to exhibit the greatest fury and jealousy, and generally results in his amorous passions being aroused to the required extent. Nor does the mare, notwithstanding she has small chance of showing her objections, always, lend her willing co-operation to the misalliance with the jack. This necessitates the services of the teaser being requisitioned, after which the mare is blindfolded and a jack is substituted for the stallion. However, the jack breeders know their animals so well that very little time is lost."

These observations seem to me to bring out very clearly the following points of technical psychological interest:

1. A remarkable keenness of the sense of sex-recognition in the jack.

2. A large *psychological* element, which has certainly some points of resemblance to similar elements in human sex behavior,[1] in the sexual activity of the jack.

3. Evidence of association in the sex behavior of the jack, which would appear to be of significance in a genetic study of the origin of sex fetishism.

Biological Laboratory, Maine Agricultural Experiment Station

---

[1] Cf. Havelock Ellis. The Psychology of Sex. (Philadelphia) *Passim.*

A SET OF BLIND WHITE RATS WHICH COULD NOT LEARN THE MAZE

HENRY FOSTER ADAMS

During a series of experiments performed at the University of Chicago during the years 1910 and 1911, the writer found a set of three blind rats which could not, or at least did not, learn the maze during a total of 182 trials. As no comment upon a phenomenon of like nature has come under my observation, it seemed worth while to mention it.

Originally there were seven rats, six females and one male, all mature and healthy. They were blinded by removing the eye-ball. All recovered promptly and were set to work to learn the maze.

During the course of the experiment, two of the rats died, so their records are not included. The disease which carried them off is, I believe, a relatively common one among white and black and white rats. First there is a sluggishness, a loss of appetite and general listlessness. This is followed in a day or two by other symptoms, the most prominent of which is a persistent twisting of the neck, so that the head is turned sideways in an abnormal manner. The head is turned more and more from day to day. Finally the animal finds it difficult to stand, is almost incapable of walking and, if it attempts to do so, often rolls over and over on the floor of the cage. Since the symptoms are somewhat similar to those following semicircular canal disturbances, it is thought by some that the disease is due to a "cold" which has settled in those organs. So far as I know, this is mere supposition. The disease is generally fatal, though there have been some cases in which the animal so afflicted has recovered.

One of the rats in this set which finally learned the maze was finally carried off by this trouble. During the first stages of the disease, it was still run in the maze. The animal had "forgotten" the labyrinth entirely. Not only that, but it ran at full speed ahead, bumping into blind alleys, partitions and the like. Whenever it got to its feet, it ran in the direction

in which it was headed until it brought up again against some obstruction.

Of the five rats which were left alive, two eventually learned the maze; the other three did not. Following is the time and error record, as far as it was kept, for the first 120 trials out of the total, 182. During a part of the experiments, the error record of the three rats which could do nothing with the maze was not kept as they often went up above 200 errors. The trials are averaged by 10's to save space.

Trials	Rats which did not learn maze		Rats which did learn maze	
	Time	Errors	Time	Errors
1–10............................	14.60	88.46	6.59	38.95
11–20...........................	6.26		2.60	10.10
21–30...........................	9.90		1.39	3.70
31–40...........................	5.85		2.35	11.95
41–50...........................	4.26		1.68	6.15
51–60...........................	1.79	13.79	.81	.90
61–70...........................	2.88	25.28	1.33	3.20
71–80...........................	4.00	25.75	.95	1.70

Up to this point in the experiment, the maze had been covered with a glass top, but here a wire screen was substituted for it. The records of the rats which did not learn the maze is continued below.

	Time	Errors
81–90............................	4.66	17.80
91–100...........................	2.66	10.50
101–110..........................	2.24	11.70
111–120..........................	2.97	18.30

The record continues until the 182nd trial. It is not given below, because the rats never came any closer to learning the maze than the above record shows.

There were certain peculiarities in the behavior of the rats throughout the experiment. They were all very slow in their movements while in the maze. The fastest time that any one rat made was 15 seconds. And that record was made by only

one rat on one trip. All of the other records were considerably slower. With another set of blind rats which were used immediately after this set, all of the group made the trip in 10 seconds or under consistently. The time spent in getting to the food box by rat 3, which learned the maze perfectly, is quite irregular. It varies from 2.11 minutes to .30 minutes for trips without error.

Another peculiarity is the slowness with which the two successful rats learned the maze. The second set of blind rats, used in the same maze, were able to go five successive times without error with an average of 20 trips, the slowest one having learned it on the 23rd trial, the best on the 17th. Applying the same criterion to the first set of blind rats, we find that the better of the two had learned the maze on the 49th trial, the other on the 63rd.

To save time in the number of days spent in the learning process, I ran the rats twice a day from the 25th to the 62nd trip. This seemed to affect the two rats which did learn the maze quite differently. Rat 3 continually made more errors on the first trial than on the second, often going the second time without error. Rat 7, on the other hand, made the first trial quite successfully, generally without error, but went all to pieces on the second trip, sometimes making as many as 36 errors.

After finishing with the animals, we sent them to the Department of Neurology, for a post-mortem examination. A gross examination disclosed no defects whatsoever.

A SOCIETY FOR ANIMAL PSYCHOLOGY

ROBERT M. YERKES

In September, 1912, there was established in Elberfeld a Society for Animal Psychology, the chief purpose of which is to promote the investigation of the mental life of the mammals, and especially of dogs, apes, and elephants. It is hoped by the founders that an Institute for Experimental Animal Psychology may be established and that numerous investigations may be encouraged in various ways by the Society.

The organization consists of members, fellows, and founders. Members pay no dues; fellows pay eight marks per year; and founders make a single contribution of at least one thousand marks.

The officers of the Society are Prof. H. E. Ziegler, Stuttgart, President; Dr. P. Sarasin, Basel, Vice-President; Karl Krall, Elberfeld, Secretary; Geh. Kommerzienrat Aug. Freih. von der Heydt, Elberfeld, Treasurer; and the following directors: Dr. R. Assagioli, Florence; Prof. Dr. H. von Buttel-Reepen, Oldenburg in Gr.; Prof. Dr. H. Kraemer, Hohenheim-Stuttgart; Prof. Dr. A. Besredka, Paris; Prof. Dr. Ed. Claparède, Genf; and Dr. William Mackenzie, Genoa.

The Society has already begun the publication of proceedings, "Mitteilungen der Gesellschaft für Tierpsychologie," under the directorship of Professor Doctor H. E. Ziegler, Stuttgart. The first number of the first volume appeared in 1913. The publication is to appear quarterly and to be sent free of charge to fellows of the Society.

The first number contains, in addition to an announcement of the Society for Animal Psychology and a list of the members, two brief articles concerning the trained horses of Elberfeld. In the first of these articles, explanations by eminent authorities of the behavior of Mr. Krall's thinking horses are offered, and in the second, Mr. Krall himself presents an account of the behavior of the blind horse, Berto.

This is the first Society for the promotion of the experimental study of the psychology of animals to be founded, and it is greatly to be hoped that those who are interested in the subject, no matter where they happen to be located, may join the organization as fellows, and thus further its work and keep in touch with the progress of investigation through the proceedings of this Society.

MODIFIABILITY IN THE BEHAVIOR OF THE CALIFORNIA SHORE-ANEMONE *CRIBRINA XANTHOGRAMMICA* BRANDT

WILSON GEE

Laboratory of Experimental Zoology, University of California

INTRODUCTION

No feature of the behavior of sea-anemones has received more consideration from biological investigators than have the feeding reactions of these interesting animals. Yet there are few parts of their répertoire of responses about which there is more uncertainty existing than about the real explanation of their modified behavior in relation to food. It was with the idea of throwing additional light on this matter that the researches reported in this paper were begun. In the main, they were conducted in the zoological laboratories of the University of California. Many valuable observations were made during a two weeks stay at the Hopkins Sea Side Laboratory of Leland Stanford Jr. University.

The writer wishes to express here his thanks to Professor S. J. Holmes for the suggestion of the problem and for the kindly help and interest which he has contributed to the work. To Professor Harold Heath of Stanford University he acknowledges many courtesies during his brief stay at the Hopkins Sea Side Laboratory. For the identification of the material used he acknowledges his indebtedness to Professor H. B. Torrey of Reed College.

HABITAT AND HABITS

Cribrina xanthogrammica Brandt is the common shore anemone of the Pacific Coast of North America, and its recorded dis-

tribution ranges from Sitka, Alaska, to as far south as Panama. It commonly occurs in great masses, entirely covering the sides of rocks, and thus affording a great abundance of easily obtainable material. This species is relatively easily kept in good condition in the laboratory provided the sea water in the dishes is frequently changed and the animals kept in a cool room. The size of the individuals varies considerably, depending largely upon the age of the anemone. Individuals from a few millimetres diameter to several centimetres can be secured, though those about five centimetres in diameter were found most suitable for the greater part of the work presented in this paper.

At low tide, the thousands of *Cribrina* exposed on the rocks are in a contracted condition, retaining sufficient water to keep the body tissues in good shape in spite of the desiccation to which they are subjected. When the anemones are strongly stimulated, much of this water is expelled, finding its way out through the mouth opening, the tips of the tentacles, or of the tubercles with which the column and the edge of the disk are covered. Pickering has called attention to this habit in *Bunodactis artemisia* and Verrill has noted the same thing in *B. Dowii*. Torrey (1906) has observed this reaction in *Cribrina xanthogrammica*, and considers that "permanent openings probably exist, although difficult to find in sections." This response must occur quite frequently in the life of the animal, since any agency which causes a close contraction of the body must necessarily cause the discharge of the surplus water contained in the gastrovascular cavity. The expulsion occurs at the points of least resistance in the body, and it appears to me that the openings at these points represent temporary ruptures which in the economy of the individual are soon repaired.

The masses of this species of anemone when exposed on the rocks blend to a quite marked extent with the sand and gravel scattered around them. This is largely due to the habit which *Cribrina* has of attaching the tips of the tubercles distributed over the column of its body to small gravel, pieces of shell, spines of sea-urchins or any similar material with which they chance to come in contact. The concealing effect is often so great as to cause one to quite overlook large masses of material in the search for anemones. After the specimens have been

kept in the laboratory for a few days, these particles of foreign material are almost all shed. In the tide-pools, specimens in an expanded condition were injected with substances such as potassium chloride and beef juice, and in many cases, immediately dropped the attached pieces of debris. These facts would seem to indicate that a certain tonus of these tubercles is necessary for them to continue to hold the covering with which they have decked themselves. That there is a changed responsiveness in animals removed to the laboratory for a few days as contrasted with those remaining in the normal habitat is a fact too obvious to escape the notice of any one who has experimented with anemones. Bohn (1907) has made this fact clear in his discussion of the diverse factors influencing general responsiveness in several species of anemones on which he worked.

In tide-pools, numbers of anemones may be found expanded during the day, thus indicating that this species of anemone remains open under the influence of strong sunlight. This conclusion is further substantiated by the experiments on the light reactions of specimens kept in the laboratory.

FOOD

Many times the attempt was made to have specimens kept in the laboratory to accept stones and perfectly clean pieces of filter paper handled with clean forceps. The tentacles in many cases would adhere to the objects and incline towards the mouth opening, but not with any considerable vigor of response, and in every case, the proffered objects were eventually refused. No difficulty was experienced, however, in having the anemone take in pieces of filter paper soaked in oyster or clam juice.

When specimens in an expanded condition in the pockets among the rocks along the shore were given apparently clean stones loosened in the sea water around them, in dozens of cases, they grasped them with their tentacles and took them into the gastrovascular cavity. One large anemone accepted a stone as large as a pigeon's egg, and apparently perfectly clean. Fair sized crabs were taken in entire by the larger anemones, as well as detached chelae of adult specimens of the rock crab, *Cancer antennarius*, and kelp crab, *Epialtus pro-*

ductus. Limpets were rapidly taken in and constitute one of the possible if not common foods of the anemone. Small marine gasteropods were also readily accepted, even though the mollusc had retracted and shut its shell with the operculum. Nereid worms and other marine annelids were in many cases held successfully by the tentacles and taken into the gastrovascular cavity. Even pieces of the foot and column of other anemones were accepted by members of the same species. In fact *Cribrina xanthogrammica,* when in its normal habitat seems to be not at all discriminating in regard to its food. The normal condition of the anemone in the tide-pools examined seems to be always that of hunger. That from the ingestion of inert bodies, such as stones, the anemone is likely to receive a certain amount of nutriment from the encrusting plant growths and minute animals has been suggested by Torrey (1904) in his paper on *Sagartia,* and my observations lead me to extend his suggestion to *Cribrina.*

In the material extruded from the gastrovascular cavity of specimens of *Cribrina* after being brought into the laboratory is to be found a variety of remains. This material from more than a dozen specimens was carefully examined, as well as the contents of the cavity of a couple of dozens of dissected specimens. The contents of the digestive cavity are usually to be found enveloped in the midst of a copious matrix of mucus. The extruded material is always surrounded by mucus, and usually is in the form of a somewhat spherical mass. Spines of sea-urchins, small gravel, chelae of crabs, remains of various of the smaller crustaceans, such as amphipods, isopods, and *Hippolyte,* and numerous small mollusc shells tell the story of a general wholesale engulfing on the part of the anemone when the waves were washing over it. To what extent some of this engulfed material affords nutriment is a doubtful matter and involves the question of the digestive abilities of the sea anemone, a subject which has not formed a part of this investigation. On breaking apart several of the detached chelae of the crabs which were taken in the extruded material the only content was found to be a small quantity of mucus. Whether these chelae contained upon being ingested the muscles which they have normally is a matter which would have to be tested by digestion experiments.

REACTIONS TO LIGHT

The literature on the reactions of sea anemones to light indicates that by far the greater bulk of these forms remain contracted during the major portion of the day, expanding only under the influence of darkness or during the hours of early dawn and twilight. Hargitt (1907) has called attention to the few observations which have been made on the sea anemones in relation to light. According to the Hertwig brothers (1879), Quatrefages (1842) working on the species of *Edwardsia* found that rays of light from a lamp concentrated upon the specimens produced partial retraction. Haime (1854) observed in species of *Cerianthus* that bright sunlight produced a contraction into their tubes, expansion occurring when the light became less intense. It was the experience of the Hertwigs (1879) that from their observations on the deep-sea form, *Cladactis costae* this species was more or less contracted during full daylight, and expanded as the light became less intense. Jourdan (1889) records a similar condition in a species of *Peractis* upon which he experimented.

Hargitt (1907) found in *Eloactis producta* that: "It only required a few observations to determine beyond doubt that only in a light of low intensity, such as twilight, or in the aquarium under the rather dim light of an incandescent lamp at some distance, did the specimens protrude their oral portions and tentacles and show any degree of activity." The same worker found a like condition to hold in the case of *Sagartia leucolena*. *Metridium* he records as rather indifferent in its responsiveness to changes in light intensity.

Jennings (1905) records *Aiptasia annulata* as "very sensitive to light, expanding in darkness, but contracting after a few seconds when exposed to strong light."

Bohn (1907) discusses the light reactions of several species of sea anemones and finds them very variable, dependent upon many conditions. In some of them he finds a persistence of an impressed diurnal rhythm for three or four days after removal from the sea.

In specimens of *Cribrina xanthogrammica* the writer observed that upon coming into the laboratory in the evening about seven o'clock, the bulk of some fifty or more specimens kept in aquaria were contracted. During the day they had been noted to be

persistently open. Some manifestations of individual idiosyncrasies were observed among the specimens, since a few of them were closed sometimes, even in spite of the daylight. However, these cases were so rare in occurrence as to make them of negligible significance. Even the most closely contracted specimen, however, could be opened under the influence of a light intensity of 32 candle power. This was tried upon a whole dish of a couple of dozens of specimens which had contracted from the effects of darkness, and by shifting the light every individual was caused to expand fully, some of the more persistently closed ones requiring from a half-hour to an hour of exposure.

This species of anemone is brightly colored; the disk may be a greenish white to green, or even a brown or pink, the tentacles partaking of much the same color. Torrey (1906) says in regard to this color: "The characteristic green color of the species is found only in individuals exposed to the sun. It is due to the presence of a unicellular alga in the endoderm of the column wall, mesenteries and tentacles. Where sunlight does not penetrate, as under wharves (Calkins), or in caves, the algae, though present, do not develop so luxuriantly as in the more exposed situations, and the polyps are correspondingly pale." It may be that in the relations of the alga to the anemone we have the explanation of its apparently exceptional behavior to light.

In order to test the possible persistence of rhythms, both tidal and diurnal, a half dozen specimens were kept for five days under both constant dark and constant light. A second series of experiments was conducted with this same end in view, and these two dozen specimens showed so far as I was able to determine, no impressed rhythmical behavior. Observations were made at intervals of three or four hours usually, and from eight o'clock in the morning to eleven o'clock in the evening. Under constant darkness, in the first experiment made, except for the expansion of an occasional specimen for a few hours, the individuals remained persistently closed for over a week. After this time there were decidedly irregular periods of contraction and expansion. Specimens kept under constant light showed a uniform continuation of the expanded condition, contracting only on the sixth day, and then as the result of an in-

crease in temperature in the water rather than from the influence of light. The first series of experiments was conducted on specimens which had been kept in the laboratory for about a week, in order that they might have time to become acclimated somewhat to laboratory conditions. The second series was, however, carried out on specimens allowed only one day in the laboratory in order that they might become attached and normally expanded. The uniformly closed condition under the influence of darkness was even more completely shown in these individuals fresher from the sea-side. The specimens kept under constant light remained persistently expanded both night and day. Control experiments of individuals taken from the same lots were carried on in each case, the conditions for these being that of normal day and night illumination. These showed the specimens to remain in each case expanded during the day, and contracted during the night.

The following record shows the results in total darkness for the first two days of the second series of experiments mentioned above. The results for the succeeding three days of the experiment being the same as given for the second day, that is, all closed, it is unnecessary to include these.

November 11th.

1 :00 P. M.   All six fully expanded (experiment begun).
2 :30   "   One partially contracted.
6 :00   "   Four well closed, one partially open, one completely open.
9 :30   "   Five well closed, one open.
11 :00 "   Two partially open, four closed.

November 12th.

8 :00 A. M.   All specimens closed.
2 :00 P. M.   "   "   "
5 :00   "   "   "   "
7 :00   "   "   "   "
9 :30   "   "   "   "
11 :00 "   "   "   "

Thus in *Cribrina xanthogrammica* the evidence seems to point towards the contraction and expansion as resulting very largely

from the direct action of the light rays. There seems to be indicated no persistence of rhythm in this species, either tidal or diurnal. The specimens from which these data were derived, however, were secured from Baker's Beach, San Francisco Bay, and while this location is only a short distance removed from the Golden Gate and the open sea, still the specimens here do not get the full effects of the tides as experienced along the unprotected ocean front. For this reason the evidence may be insufficient to state positively that tidal rhythms are not established in *Cribrina* as was found by Bohn (1907) in his work on several species of anemones. However, the evidence does lead one to the conclusion that the contraction and expansion in this species is largely the result of the direct action of the sun's rays, due perhaps to the symbiotic relation of the algae contained in the cells of the body of this species of anemone. The higher temperatures, desiccation, toxic solutions of sea water, and such factors are effective also in producing contraction, as was found by Bohn in his experiments on sea anemones.

FEEDING REACTIONS

Parker (1896) found in *Metridium* by feeding alternate pieces of meat and filter paper soaked in meat juice to the tentacles of one side of the disk, after a few times, the filter paper was refused, though the meat continued to be accepted. Finally, the tentacles of that side of the disk refused the meat also, but when this was offered to the tentacles of the opposite side, they accepted both the meat and soaked filter paper like the side first fed. In accounting for this behavior, Parker (1896) says: "The successive application of a very weak stimulus is accompanied, not by the summation of the effects of stimulation, but by a gradual decline in these effects till finally the response fails entirely."

Jennings (1905) found in *Aiptasia* that refusal of the filter paper was caused more rapidly by feeding meat alone for several times than by feeding successively filter paper alone or alternately filter paper and meat. He fed specimens of this genus several pieces of crab meat in succession to the tentacles of the left side only. When these tentacles became irresponsive, the meat was offered to the tentacles of the right side and these immediately accepted it. After a short period, meat was again

slowly accepted by the tentacles of the side first fed. However, these tentacles soon became irresponsive, and the food was offered again to the tentacles of the right side, which had reacted only once and that fifteen minutes before. These were found to react just as did those of the left side, hanging back from the disk along the column. Jennings concludes as the result of this behavior "that the animal is a unit so far as hunger and satiety are concerned. If the satiety has arisen through the activity of the tentacles of one side, the tentacles of the other side are equally affected by it. It is the general progress of metabolism that is the chief factor in determining the reactions to food." In discussing the comparative responses of the hungry and well individuals he says: "The well fed animal reacts less readily and strongly to simple mechanical shock. If touched with a needle, the well fed individual either does not react at all, or contracts very slightly while the hungry specimen reacts suddenly and powerfully. A slight disturbance in the water has no effect on the well fed individual while the hungry one contracts strongly. To chemical stimuli the same relations apply."

Allabach (1905) in working on *Metridium* tried feeding alternately pieces of meat and soaked filter paper, not allowing the filter paper to be swallowed. Refusal of the filter paper occurred just as in the cases where it had been swallowed. Thus the effect of the paper after it reaches the digestive cavity cannot be the cause of its rejection. Filter paper was also refused after the tentacles of the same region of the disk had several times accepted meat. "This result was likewise reached if the animal was not allowed to complete the swallowing of the meat, the latter being removed after it has passed into the oesophagus. This of course shows conclusively that the loss of hunger is not the cause of the change of reaction towards the paper." In a succeeding portion of the paper Allabach says: "It appears evident therefore that it is the reaction of the animal, not the precise character of the stimulus that causes the fatigue. This is perhaps what should be expected when the nature of the food reactions is taken into consideration. In taking food the region in contact with the food produces a very large quantity of mucus, enveloping the food body. It is not surprising that successive immediate repetitions of this excessive production of

mucus gradually exhausts the region. As is usual in fatigue, strong stimuli may produce reaction for some time after weak ones have failed. The fatigue thus caused usually lasts only two to five minutes. After this period has elapsed the fatigued region is frequently as ready to take food as before—provided the animal is still hungry."

FEEDING REACTIONS OF *CRIBRINA XANTHOGRAMMICA*

The responses involved in food taking in *Cribrina* are much the same as those so excellently described by Jennings for *Stoichactis helianthus*. If a piece of fresh oyster is given the tentacles of a hungry *Cribrina* these immediately adhere to the meat, and bending over with it, hold it tightly against the surface of the disk. A depression of the disk takes place in the region of the food, and in this way the mouth opening is brought nearer to the piece of oyster. This opening in the meanwhile has become enlarged and the bladdery lobes of the stomodaeum are extruded towards and around the food. The tentacles release their hold, and the food is taken into the gastrovascular cavity by the muscular action of the stomodaeum. Depending very largely upon the size of the piece of meat, either a part or the whole of the disk and tentacles may contract during the feeding reaction. For a small piece, usually only a portion of the disk is involved in the food taking if the anemone is of fair sized proportions.

It occurred to the writer that there might be some way of securing the same effect on the metabolism of the anemone as is produced by the food without the muscular effort incident to food taking. Thus the factor of muscular fatigue as such could be eliminated. Wyeth's beef juice, for which the manufacturers claim "that it contains all the albuminous principles of beef in an active and soluble form" was the first substance used. A dilution of this, two parts of beef juice to eight parts of sea water, was forced by means of a pipette into the gastrovascular cavities of several anemones. It was found impossible to prevent an ejection of this material to a certain extent by the contraction of the anemone, and the consequence was a diffusion of the beef juice over the tentacles, with an immediate

copious secretion of mucus from the surface of the tentacles and also from the gastrovascular cavity. The anemone contracted strongly as the result of the stimulus, but in a short time expanded. The tentacles were coated with mucus, some of them tending to remain in bunches as a result. Application of contact stimulus showed that they were practically insensitive to stimulation of this character. Many of the tentacles hung flaccidly over the edge of the disk.

As far as possible, the mucus was removed entirely from the disk and tentacles, and the animals placed in a dish of fresh sea water. Pieces of oyster given to the tentacles were persistently refused, though when placed over the mouth opening they were slowly accepted. In a few hours the tentacles were observed to again become responsive to contact stimuli. After a varying period of from one to three days, all of the specimens had so far become recuperated as to readily accept food given to the tentacles.

Next a rather strong solution of peptonoids was forced into the gastrovascular cavity of several specimens with much the same results as were secured in the case of beef juice. A concentrated oyster extract obtained from macerating fresh oysters was tried, the tentacles in this case showing the same flaccidity and excessive mucus secretion as in the case of the beef extract, though to a less degree. This lessened degree of secretion was evidenced in the relative quantity of mucus secreted as the result of injection, as well as by the earlier recovery of the individuals so treated. After a period of about one day, provided the animals were kept in a cool room, the tentacles of most of the specimens had become thoroughly responsive and would accept food offered them.

Parker (1905) in his work on the reversal of ciliary action in *Metridium* records that a copious secretion of mucus was one of the results produced by the application of a potassium chloride solution of sufficient strength to cause reversal of ciliary movement in the region of the mouth of the anemone. This suggested the idea that there might be a number of chemicals producing a similar effect, and the results of an investigation into the effects of several solutions of varying strengths and composition are given below.

METHODS EMPLOYED

In the succeeding experiments, the animals were placed each in a separate dish, twelve centimetres in diameter. Here they were allowed to remain for two or three days so as to become thoroughly acclimatized and normally responsive. Each individual was tested to see that it accepted food before the injection of the chemical was made, and if it failed to do so, the animal was not used in the experiment.

With a thoroughly clean pipette, consisting of a glass tube drawn out to a sufficiently small point, each substance was forced through the mouth opening into the gastrovascular cavity of the animal, or over the surface of the disk and tentacles according to which was desired. As soon as the injection was made, the water was removed from the dish, the specimen thoroughly rinsed with uncontaminated sea water, and a quantity of sea water equal to the original amount in the dish placed over the anemone. The experiments were performed in the strong diffuse light of the laboratory, in order to have the animals expand as soon as possible after treatment. The mechanical part of the operation could in no way injure the body of the specimen, since the point of the pipette was not left irregular but was melted down to a perfectly smooth glass edge.

RESULTS OF INJECTION EXPERIMENTS

Pure sea water.—Some of the solutions were made up in sea water, and in order to determine what effect the mechanical part of the operation might have a dozen anemones were injected with clean sea water. Contraction was of course produced as the result of the contact stimulus, but the anemones almost immediately began to expand. Upon expansion their reactions to food, mechanical stimuli, etc., appear entirely normal. A similar result was secured upon the injection of fresh water. Thus there seems no complicating factor in this regard.

Sodium chloride.—(Normal solution in sea water and 3/8 normal in distilled water.) Immediately upon expanding after injection, the tentacles showed normal responsiveness. No mucus appears to have been secreted. The tentacles accepted food readily upon its being given to them. A 5/8 M NaCl + 1/3 M NaCl was injected also but with the same result.

Potassium chloride.—(Normal solution in sea water and 3/8 normal in distilled water.) Thorough injection produced a copious mucus secretion. At end of two hours specimens had not expanded, but the tentacles were almost totally irresponsive. When a piece of oyster is placed over the mouth, the bladdery lobes of the stomodaeum were extended and the food taken in. The following morning the tentacles had recovered almost normal responsiveness to contact stimulation, but still refused food given to them. At four o'clock of the same day the tentacles slowly accepted food offered them. The second day after the experiment, the anemones in many cases accepted food quickly, and the most of them seemed in every way, so far as discernible, entirely normal in responsiveness.

In the case of the 3/8 M KCl in distilled water, a solution practically isotonic with sea water, the anemone in three cases out of six slowly accepted food after injection and subsequent expansion. The mucus secretion upon treatment with this strength of solution was not nearly so copious as in the case of the normal solution. Consequently I am led to believe that the number of potassic ions present was not sufficiently an excess to produce an exhaustion of the mucus secretion of the tentacles adequate to prevent the acceptance of food by these through their lowered responsiveness. This view is strengthened by the fact that 5/8 M KCl + 1/3 M KCl did produce a condition to all effects the same as that produced by the normal solution of potassium chloride used. This solution of potassium chloride contained a larger number of potassium ions than did the solution isotonic with sea water. The fact that it is a solution hypertonic to sea water is not of significance, I believe, since a solution of sodium chloride of the same strength effects no change in food response. This is also an indication that the potassium ions are the factor producing the secretion of mucus and not the chlorine ions.

Mercuric chloride.—(0.2 per cent solution in sea water.) A thorough injection produced a very marked secretion of mucus apparently from all of the surfaces of the body. The individual was killed as the result of this injection, even though the sea water was changed immediately. Where a partial injection was secured into the gastrovascular cavity at fifteen minutes past nine in the morning, at noon response of the tentacles was

practically as sluggish as immediately after the anemone had expanded. At half past one o'clock of the same day, the tentacles had recovered somewhat in their responsiveness to contact stimulation, but did not show any response to food. When pieces of oyster were placed over the mouth of the animal they were slowly accepted.

In another case, the solution was forced over only the disk and the tentacles. This was done at twenty minutes past nine in the morning and at noon the specimen had not expanded. At one o'clock, however, the specimen was open, but the tentacles persistently refused food, and hung entirely irresponsive over the edge of the disk. The bladdery lobes of the stomodaeum were extruded around a piece of oyster placed over the mouth opening and this food was taken into the gastrovascular cavity.

The specimens treated with mercuric chloride recovered most slowly of all of the anemones experimented upon. The applications were made one Friday morning, and it was a week from the following Monday before many of the specimens injected would accept food given to them. On the third and fourth days after injection, a heavy film of mucus was shed from the entire surface of the body. Pavlov (1910) from his work on mucus secretion in the stomach of the dog has the following to say in regard to the excessive secretion of mucus in relation to the economy of the organism: "When potent reagents such as absolute alcohol, a o.2 per cent sublimate solution, a ten per cent solution of nitrate of silver, or a strong emulsion of oil of mustard, were introduced for a few minutes into the small stomach they produced a more or less copious, indeed in many cases enormous secretion of mucus. * * * The contrast between the intensity of the phenomenon and its short duration is really striking. One cannot help thinking that in these cases a morbid condition has not as yet been established, but rather that the pathogenic influence, had been successfully encountered and conquered before one's eyes." He suggests that in this behavior the true function of the surface epithelium has been revealed. Its copious secretions dilute the noxious substance, or form chemical combinations with it and at the same time expel it from the stomach wall.

Calcium chloride.—(Saturated solution in sea water, and 3/8 normal in distilled water.) With the saturated solution in sea water at the time of injection, forty minutes past nine in the morning, a medium secretion of mucus was produced and a semi-responsive condition immediately upon expanding. At noon the animal was almost normally responsive to contact stimulation. While in the afternoon, the tentacles of the animal had recovered normal responsiveness to contact stimulation, food given them was not accepted. The next day, however, food was slowly accepted in the afternoon, and the succeeding day, the tentacles responded entirely normally when given food. Of the four specimens tested with 3/8 M CaCl in distilled water, two showed a greater mucus secretion than the others and accepted food several hours after; the other two accepted food immediately upon expanding.

Lithium chloride.—(Normal solution in sea water and 3/8 normal in distilled water.) Comparatively little secretion of mucus was produced upon injection. The anemones appeared entirely normal upon expansion, and gave immediate and vigorous response to food given to the tentacles. The same effect was produced in the case of the specimens treated with a 3/8 M solution in distilled water.

Magnesium sulphate.—(Normal solution and 3/8 normal in distilled water.) A number of anemones injected with magnesium sulphate in considerably greater volumes than were used in the preceding experiments showed practically no secretion of mucus, but almost all of them practically total irresponsiveness to contact stimulation. The tentacles presented a more rigid condition than was the case with the other substances producing a lowered degree of tonus. This is perhaps to be attributed to a partial paralysis of the muscles coupled with a condition of anesthesia in the body of the animal. The experiment was begun at ten o'clock in the morning and by two o'clock that afternoon the tentacles contracted after several successive stimulations with a glass rod. At four o'clock in the afternoon of the same day, the tentacles had so far recovered as to become almost normally responsive to contact stimulation, but persistently refused food given to them. Food placed upon the mouth was taken into the gastrovascular cavity. Three

days after treatment the tentacles slowly accepted food, however, not in an entirely normal manner. Inclining with the piece of oyster, they dropped it over on to the disk to be accepted by the mouth.

In the case of the 3/8 M Mg SO$_4$, the individuals showed considerable variability. Three of the five specimens treated showed a similar though less intense effect to that produced by the normal solution; the other two accepted food upon expanding a few minutes subsequent to their treatment.

With regard to the action of magnesium salts Cushny (1910) says: "The magnesium salts have recently been shown by Meltzer to have a very powerful action when injected hypodermically or intravenously. The most characteristic effect is complete anesthesia, resembling that induced by the chloroform group and ending in fatal cases in paralysis of the respiratory centre."

The effect of magnesium sulphate upon anemones is known to all who have ever preserved specimens of these forms. The condition of anesthesia produced in the animal prevents its contraction upon the addition of the preserving fluid, and the specimen is secured in an expanded fixed condition. Thus the irresponsiveness of the *Cribrina* in these experiments is to be attributed to the anesthesia produced as the result of these injections. There seems to be produced also a paralysis of the muscular fibrils of the cells of the body.

EXPERIMENTS ON THE NORMAL FEEDING REACTIONS OF *CRIBRINA*

The experiments of Parker (1896) on *Metridium* were repeated on *Cribrina* and it was found that the tentacles of the left side accepted pieces of oyster given it for eight successive times. The oyster was then given to the right side and was immediately accepted. For the two succeeding times food was taken by them, but subsequent tests gave a refusal in this region. This is to be accounted for, I believe, as the effect of the diffusion of the food juices in the water causing the production of mucus in addition to that caused by the actual contact with the food. No doubt what von Uexküll would term a "withdrawal of tonus" from the tentacles to the region of the mesenteries also takes place due to the secretion of digestive

juices incident to the digestion of the food already taken in by the action of the tentacles of the other side.

As previously stated, depending upon the size of the piece of food taken in, either a part or the whole of the disk and tentacles is involved in the feeding reaction. In order to determine what effect this factor might have in the relative responsiveness of the two sides, two specimens were fed large pieces of oyster, thus causing the greater portion of the tentacles of the anemone to come in contact with them during the feeding response. The oyster was given to the tentacles of the right side, which in one anemone accepted five times successively, in the other anemone seven times. Then the oyster was offered to the tentacles of the left side of each anemone. In one case, the tentacles slowly accepted one piece of oyster; in the other, the meat was refused entirely.

An anemone which was previously tested and found to accept food quickly upon its being given opportunity to do so, was made to contract for a dozen successive times as the result of mechanical stimulation with a sterile glass rod. Oyster was then given to its tentacles, and was accepted for eight times, as many times as the average individual of those experimented upon would accept food without having been previously stimulated mechanically. This would seem to indicate that the factor of muscular fatigue is not a significant one in the modifiability in response to food, except as it is perhaps incident to a depression from mucus secretion. This experiment was several times repeated with a similar result.

The matter of giving the tentacles food and allowing them to carry it to the oesophagus and then removing it before it was swallowed was also tested. It was found that after about the normal number of times for the acceptance of food, the tentacles would fail to respond, seeming to indicate that refusal of the food material is very largely if not entirely a matter of the responsiveness of the tentacles, especially since the mouth is always, even under the most adverse circumstances ready enough to accept food given to it. Allabach (1905) has found that *Metridium* will accept food placed over its mouth until the body of the animal is gorged, and ejecting this accumulated amount, the mouth will again accept food placed over it. The same worker has tested the matter of feeding the animal but

not allowing the food to be swallowed, and says with regard to her experiments: "The fatigue thus caused usually lasts only two to five minutes. After this period has elapsed the fatigued region is *frequently** as ready to take food as before—provided the animal is *still hungry*."* My experience was, however, that in some cases, as many as seven hours were required for the animal to recover responsiveness sufficient to accept food given to the tentacles. In no case where the animal had been thoroughly fed until it refused to accept food with the tentacles of any part of the disk did I succeed in getting animals to accept food more than twice after a period of five to ten minutes, and these cases were comparatively rare. The fact that the anemone will accept food after this short period of rest is what might be expected to be the case, since the juices of the food are not sufficiently strong to entirely exhaust the tentacles through mucus secretion as the stronger substances have been shown to do. One or more partial recoveries before complete exhaustion is what might be looked for even in the matter of mucus secretion. This being the case, I think that there is no necessity for the belief that this reaction is due to the fact that the animal is "still hungry," but rather that it is due to the rallying power of the tentacles before complete exhaustion.

FEEDING REACTIONS IN NORMAL HABITAT

A two weeks' stay at the Hopkins Sea Side Laboratory, Pacific Grove, California during a period when the tides were exceptionally favorable permitted not only observations on the normal food habits of the anemones recorded in a previous portion of this paper, but also an opportunity to try the effects of injecting the specimens in the tide-pools with certain of the substances used in the laboratory experiments.

After injecting specimens in an expanded condition in the pockets among the rocks at low tide with the same strength of beef juice previously used, there was noted the same excessive secretion of mucus, almost total irresponsiveness to stimulation, and total neglect of food on the part of the tentacles as was found in the specimens kept in the laboratory. Potassium chloride gave even more marked results of depression than the

---

* Italics mine.

beef juice.   Injection with a strong sodium chloride solution seemed to alter in no way the normal responsiveness of the animal either to food or to contact.   The animals used in these experiments were first tested to see that they would take food before the experiment was performed, with the result that they immediately availed themselves of the opportunity.   In fact, I have yet to see an anemone of this species in an expanded normal condition in their native habitat refuse to accept food; for they all appear to be in a condition of quick responsiveness to stimuli of the various kinds.

RÔLE OF MUCUS SECRETION

Duerden (1906) in a most interesting paper on the rôle of mucus in corals has shown that it serves two general functions. (1) The protection of the polypal surface from foreign objects and in keeping it clean, and (2) the entanglement and ingestion of prey and food substances.   He notes that nutritive substances and extractives placed upon the polyp increase the amount of mucus exuded.   The same result is secured, though to a less degree, by mechanical stimulation.   He says: "Not only does the mucus serve as a protection to the polyp under adverse circumstances and assist in getting rid of foreign substances which may fall upon it, but it is of much importance in the process of nutrition, by serving as a vehicle or means of conveyance of nutritive substances to the mouth and down the gullet."

Perhaps the rôle of mucus in the actinian polyp is not essentially different to that played by it in the corals.   The idea of Pavlov (1910) quoted in a preceding paragraph to the effect that the secretion of mucus in the stomach of the dog upon the application of potent reagents is protective in that it dilutes or neutralizes the noxious substance is certainly suggestive in its application to the results secured in *Cribrina*.   We must conclude, I believe, that the copious exudation of mucus upon the application of such substances as potassium chloride and mercuric chloride serves in a decidedly protective manner.   I have too little evidence to say to what extent the mucus acts as a food securing factor.   In the extruded material of the anemones examined, many smaller organisms were found, and it is quite possible that these might accumulate in the mucus film always over the surface of the anemone until they had acquired a

sufficient nutritive strength to cause the reversal of ciliary action and the consequent ingestion of the mucus material. Certainly the conditions under which an anemone is fed in the laboratory are most unusual, and it may be that there are substances in the oyster, crab, or other meat employed in the feeding experiments, which are more or less injurious in nature to the anemone, and that these substances produce the copious mucus secretion. There does seem to exist some relation between the reversal of the beat of cilia and the secretion of mucus, since substances producing the one, usually produce the other.

DISCUSSION OF RESULTS

Removal of the mucus.—One possible explanation of the phenomena described in the preceding experiments might be thought to be that the mucus forms a coating over the tentacles and that this acts as a mask to lower the responsiveness by covering the sensory cells. That this is not the case can be quite easily demonstrated by removing all of the mucus with a camel's hair brush from several tentacles and then stimulating these. They will be found to be as irresponsive as the tentacles about them on which the mucus still remains. Also, even upon very strong contact stimulation immediately after expansion, the tentacles remain perfectly flaccid, in many cases, a condition which would not hold true were the insensitiveness due solely to the masking effect of the coat of mucus.

Muscular fatigue.—That the loss of responsiveness on the part of the tentacles after much food has been taken in is not due to fatigue resulting from the activity of taking in food on the part of the muscular fibrils has been shown by Allabach in the following experiment. An anemone was fed on one side of the disk till the tentacles of that region refused to accept food. Meat given to the opposite side was not taken at all, though these had not been active in food taking. A clearer indication of the fact that muscular fatigue alone as the result of food taking plays but a negligible part in the decrease of response is shown by the experiment described in an earlier portion of this paper. Anemones made to contract as the result of contact stimulation with a sterile glass rod for as many times as they normally accept food showed no decrease from the average of times other anemones had been found normally to

accept food. Upon watching an anemone in its normal habitat one observes the dozens of times that it partially contracts and expands under the stimulation of the waves and it is perhaps due to this type of response enforced upon the animal by the conditions of its very existence that the muscular fibrils do not become so easily fatigued. Certainly also a single injection of beef juice causing the animal to contract only once cannot cause the muscles to become fatigued solely through the power of a single contraction. There seems to be some other more fundamental reason involved, though no doubt the marked contraction following such a treatment may to a certain extent be an accessory factor.

Diminution of responsiveness from mucus secretion.—Parker's conclusion from his experiments on the feeding reactions of anemones is "that the successive application of a very weak stimulus is accompanied, not by the summation of the effects of stimulation, but by a gradual decline in these effects till finally the response fails entirely." Jennings concludes in regard to the modifiability in *Stoichactis helianthus* and *Aiptasia annulata* that "it is clear that the animal is a unit so far as hunger and satiety are concerned." In case the satiety has arisen through the efforts of the tentacles of one side, the tentacles of the other side are equally affected by it. The chief factor in determining the reaction to food is the general progress of metabolism.

Allabach (1905) observes in her paper on *Metridium* that in taking food the region in contact with the food produces a very large quantity of mucus enveloping the food body. Holmes (1911) in discussing the claims of Fleure and Walton (1907) for the power of associative memory in the sea anemone says: "It is possible that the seat of the change of behavior is in the tentacles alone. Allabach has shown that after the tentacles of *Metridium* have responded to a stimulus a few times their production of mucus becomes much diminished and this probably affects their subsequent activity. If this factor would modify the irritability of the tentacles for some time it might explain the change of behavior."

There can be no doubt that the reaction accompanying the excessive secretions of mucus as the result of beef juice and potassium chloride does alter the irritability of the tentacles.

Just how the mucus secretion affects the responsiveness of the muscular fibrils has not been determined in the present work. There seems to be a disturbance of the balance of nutrition in the cell and the muscular fibrils of that cell suffer as a consequence. An important agency in effecting the lowered tonus would seem to be a withdrawal of nutritive materials from the muscular elements and the tentacles hang flaccidly along the edge of the disk. The relation of the neurofibrillar system of the anemone to the secretion of mucus is scarcely possible of determination. There is a possibility that the changed responsiveness in the anemone may be due to the effects produced in the neurofibrillar system by the chemicals employed. There may be even a condition similar to anesthesia produced.

It would certainly seem to the writer that from the data presented in this paper, there is no valid ground for stating that the modified behavior in relation to food is due, as Jennings (1905) contends, to the animal's acting as a unit in "satiety." If the general condition of satiety affects the organism as a "unit" why should it be that even after being gorged with food, the gastrovascular cavity ejecting the material through the mouth opening, the mouth continues to accept food? And why is it that the tentacles of the animal can be made irresponsive to food without any of this food entering the gastrovascular cavity? Then, too, Parker (1896) has found and Jennings (1905), in certain cases, as well as Allabach (1905) and the present writer that upon the tentacles of one side being fed to refusal, the tentacles of the opposite side of the disk will accept food. The view that the seat of the modified responsiveness lies very largely in the individual tentacles is more clearly in accord with what is known of the structural organization of the sea anemone than that the animal acts as a unit. The successive applications of pieces of food, through the accompanying mucus secretion serves to lower the responsiveness of the tentacles, and a gradual decline in this responsiveness is produced till finally the feeding response fails entirely on the part of the tentacles.

SUMMARY

The species of anemone studied, *Cribrina xanthogrammica* Brandt usually remains expanded during the day and contracted during the night. It is suggested that the presence of numerous

algal cells in the endoderm of the column wall, mesenteries, and tentacles probably tends to make such behavior adaptive in character.

There seems to be no impressed diurnal or tidal rhythm in specimens of *Cribrina* removed to the laboratory; for when placed under uniform illumination this species remains expanded for several days continuously, and when subjected to darkness, contracts and remain contracted for a like period.

In their native environment, all of the anemones examined appeared to be hungry, and in many cases, quite readily swallowed apparently clean objects such as stones. The food of *Cribrina* was found to be very varied in its kind.

The introduction of a solution, two parts of beef juice to eight parts of sea water, into the gastrovascular cavity of the anemone produced a copious secretion of mucus, accompanied by a lowered responsiveness of the organism. Food offered to the tentacles of an anemone so treated was rejected.

Much the same reaction, though to a less degree, was secured upon the application of a concentrated extract of fresh oyster. A quite marked mucus secretion and a proportionate degree of depression was produced upon treatment with both potassium chloride and mercuric chloride.

Solutions of sodium chloride and lithium chloride isotonic with the potassium chloride were found to produce only negligible effects upon the anemones treated. The tentacles of these accepted food immediately upon the expansion of the anemone.

Muscular fatigue seems to be of little importance in the modified responsiveness to food.

It was found possible to produce a condition of irresponsiveness to food on the part of the tentacles by feeding these large pieces of oyster successively and not allowing this meat to be swallowed.

The altered behavior in relation to food on the part of the tentacles seems to be due to the lowered responsiveness accompanying mucus secretion. This depression is perhaps caused by the disturbance of the balance of nutrition in the cell; perhaps as the direct effect of the substance employed on the neurofibrillar system of the anemone.

The evidence seems to warrant the conclusion that the modified behavior in relation to food is due rather to a gradual decline

in the responsiveness of the tentacles to food than to the animal's acting as a "unit" in hunger and satiety.

BIBLIOGRAPHY

ALLABACH, L. F.   Some points regarding the behavior of Metridium.   Biol. Bull.,
1905.   **10**, 35-43.
BOHN, G.   Introduction a la psychologie des animaux a symetrie rayonee.   Bull.
1907.   de l'Insitut Gen. Psychol., **7**, 1-87.
CUSHNY, A. R.   Pharmacology and therapeutics.   10th ed.   744 pp.   Philadel-
1910.   phia.
DUERDEN, J. E.   The role of mucus in corals.   Quart. Journ. Micr. Sci., **49**, 591
1906.   614.
FLEURE, H. J. and WALTON, C. L.   Notes on the habits of some sea anemones.
1907.   Zool. Anz., **31**, p. 212.
HARGITT, C. W.   Notes on the behavior of sea anemones.   Biol. Bull., **12**, 274-
1907.   284.
HOLMES, S. J.   The evolution of animal intelligence.   Henry Holt and Co., pp.
1911.   296.
JENNINGS, H. S.   Modifiability in behavior.   I. Behavior of sea anemones.   Journ.
1905.   Exp. Zool., **2**, 447-472.
JOURDAIN, E.   Les sens chez les animaux inferieurs.   Paris.
1889.
LOEB, J.   Studies in general physiology.   Univ. of Chicago, Decennial Publ., vol.
1905.   **15**,, part II, pp. 440-449.
PARKER, G. H.   The reactions of *Metridium* to food and other substances.   Bull.
1896.   Mus. Comp. Zool. at Harvard Col., **29**, 107-119.
1905.   (a) The reversal of ciliary movement in metazoans.   Amer. Journ.
           Physiol., **13**, 1-16.
           (b) The reversal of the effective stroke of the labial cilia of sea ane-
           mones by organic substances.   *Ibid.*, **14**, 1-6.
PAVLOV, I. P.   The work of the digestive glands.   2nd Eng. ed., London.   pp.
1910.   238.
TORREY, H. B.   On the habits and reactions of *Sagartia davisi*.   Biol. Bull., **6**,
1904.   203-216.
1906.   The California shore-anemone, *Bunodactis xanthogrammica*.   Univ. of
           Cal. Publ. in Zool., vol. **3**,, no. 3, pp. 41-45.

THE QUESTION OF FORM PERCEPTION

WALTER S. HUNTER, Ph.D.

The University of Texas

Two figures

The incentive for the writing of this note was furnished by the recent publication of two studies on form and size perception in animals.[1] The question I wish to raise is this: Is there any evidence that animals discriminate form, as that term is ordinarily used? Indeed I shall go farther and ask whether it is fair to ask them to do so under the experimental conditions described.

An animal is trained to select a triangle in preference to a circle of equal area. Adequate controls are used to insure that the animal is not reacting to such extraneous cues as sound, intensity, position, the experimenter, etc. Throughout these series of controls the animal's reactions remain at a high percentage of correctness. Has it been established that a perception of form exists, or must one proceed to invert the triangle as an additional control? Bingham says:[2] "Because his studies of the reaction of other chicks to similar stimuli yielded negative results, Breed attributes the positive reactions of No. 76 to a fortunate choice of subject. Unfortunately, however, he seems to have made no control tests to determine whether or not the distribution of light on the chick's retina was influential. An inversion of a square would cause no change in the distribution of light; such a change might have been produced by turning the square through 45 degrees. A control test of this sort, however, is more easily made when a triangle is presented along with a circle. Inversion of a triangle produces a marked difference in the distributions of the light which reaches the retina, *yet the form of the stimulus is unchanged.*" Bingham

[1] Lashley, K. S. Visual discrimination of size and form in the albino rat. Jour. Animal Behavior, 1912, vol. 2, no. 5.

Bingham, H. C. Size and form perception in *Gallus domesticus*. Jour. Animal Behavior, 1913, vol. 3, no. 2.

[2] Op. cit., pp. 101-2. Italics mine.

in his own work set up, in one case, a discrimination between a triangle of 28 sq. cm. and a circle of the same area. When the triangle was inverted, the animal failed in its reactions. He concludes that the indications are "*that this discrimination is on some other basis than form.*"[3] Farther down on the same page, he says "*form in the stricter sense* has been found to have no discriminative value."

So far as I know, Bingham is the only one who has put the problem just that way, i.e., form *vs.* retinal distribution of light. The conception of "form" to which I desire to call attention is perhaps *hinted* at in Lashley's article. Lashley tested white rats (Ex. 5), on the discrimination of two lines each 2 x 60 mm. One line was horizontal and the other vertical. Positive results were obtained. The author refers continually to this as a discrimination of *forms*. The assumption underlying it all is undoubtedly that although *for the experimenter* the *illumined spaces* were identical rectangles for the animal the situation presented was one of different forms. Lashley does not develop the point, nor does Bingham, who writes later, refer to the former author's data—although Lashley cannot be interpreted as using the term "form" in Bingham's sense. (Lashley's article may not have appeared when Bingham's went to press.) The stimuli used by Lashley were *identical forms* from Bingham's point of view. Now what I wish to insist upon is this: Animals do not discriminate *form* in the abstract sense in which Bingham uses that term. Both series of experiments referred to above are concerned with *patterns*, not *forms*. I would go farther and present the hypothesis that *all* animals below man have only a more or less crude pattern vision and that this probably applies also to a varying period of human childhood.

This hypothesis presents itself for consideration under two forms: (1) Its validity under artificial experimental conditions such as are found in the experiment boxes used by the investigators above cited. (2) Its validity under conditions of a natural habitat. Let us take up these points in the order mentioned. (1) In problem boxes such as those described by Lashley and Bingham (these are of the same general nature as those recommended for the study of size and form by Yerkes and

[3] Op. cit., p. 110.

Watson[4]), the animal tested is confronted *not* by two *"forms"* corresponding to the configurations of the opal glass, but by such designs as are suggested in figure 1. The squares drawn in the figure represent the rectangular tunnels down which the animal goes in making his responses. What the animal sees is a triangle or a circle[5] each in more or less of a square setting. Now I put this question: If an animal is trained on diagrams 1 and 2, is it any wonder that he breaks down when confronted
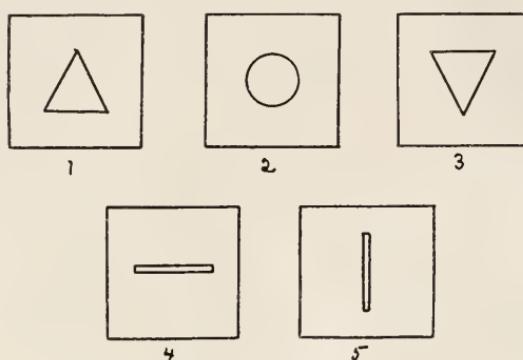
FIGURE 1. The stimuli which confront the subject in standard tests for *form* discrimination.

by diagrams 2 and 3? The problem would be puzzling to a human adult, unless he had been *told* to attend to triangularity! Furthermore if the animal is trained to discriminate diagrams 4 and 5, it does not follow that the responses are based upon the lines *per se* and not upon the whole pattern.

Apropos of this, I suggest the following: In experiments upon visual "form" perception, controls should be made in which the shape of the tunnels are varied. A discrimination could be set up, e.g., between two forms when presented at the ends of square tunnels. After controls have been used for intensity, position, etc., substitute triangular tunnels and then circular tunnels. Figure 2 shows the resulting designs which will confront the animals. Under these conditions, it should be possible to demonstrate experimentally whether the subject was reacting to the "forms" or to the entire "patterns."

[4] Yerkes, Robt. M. and Watson, Jno. B. Methods of studying vision in animals. Behavior Monographs, 1911, vol. 1, no. 2.

[5] I do not assume the perception of form by this phrasing. The wording is from the anthropomorphic standpoint for brevity's sake.

I feel that my point with respect to problem boxes is clear. It remains to indicate further that the same hypothesis is applicable, *a priori*, to discrimination under natural conditions. *"Form"* discrimination is always *pattern* discrimination. If an animal sees a triangular object, the object is not alone. It is either projected against some other "objects" in the background and hence is a part of a pattern, or it is seen *surrounded by the more or less irregular outline of the field of vision* and so is again part
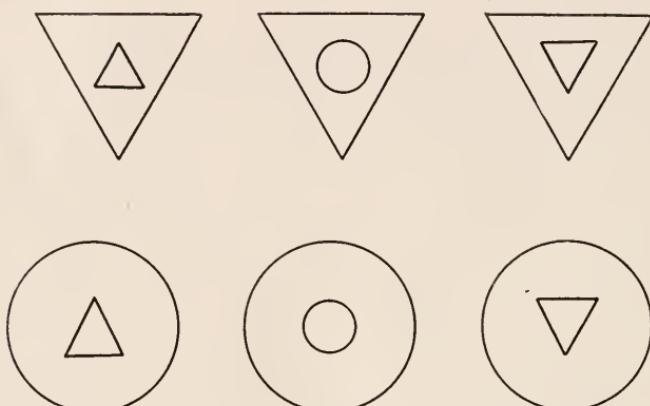
FIGURE 2. Control stimuli which should be used in the study of *form* perception in order to bring out the influence of the shape of the backgrounds upon the discrimination.

of a pattern.[6] (To be sure it is an assumption to say that the animal *can* perceive this outline; but until experiments have indicated either the existence of the more abstruse form perception or have determined the influence of the background upon which the "form" is projected, the assumption may be held as probably valid.) This influence of the shape of the field of vision upon the form of objects can be readily demonstrated by the reader upon himself. Hold a medium sized book about a foot from the eyes. Fixate the book steadily and confine the attention to noting the visual pattern of the whole experience. What one gets is almost as distinct a pattern as is shown in

[6] Külpe (Outlines, pp. 365-366) suggests a similar influence of the form of the visual field upon illusions. This theory has been tested to some extent on humans by C. W. Valentine (Brit. Jour. Psych., vol. 5, pt. 1) with negative results.

The perception of form has been studied by several students by means of objects set up in the natural environment or habitat. However, such work has never taken cognizance of the points here brought forward.

figure 1. Now rotate the book in a plane perpendicular to the lines of vision. The visual experience certainly has changed; and the more naive the observer tries to be, *the more it seems as though even the "geometrical form" of the book has changed too*! This is the state of affairs, I believe, in the animal and the young child.[7] The reader need not think that he is invited to construct a situation which is beyond the powers of animals and children. Quite the contrary. He is only asked to neglect his own developed and sophisticated knowledge of the details of his environment (which it is important to remember the animal lacks) and attempt to reinstate that which may be genetically simple.

One further point deserves comment. The discrimination of two "complexes" is often easier than that of two "simples." What the experimenter regards as *simple*, i.e., *as readily attended to*, may prove very difficult to discriminate. The fault lies in the confusion of logical and genetic simplicity. *Logically* a pattern, in that it involves an interrelation of elements, is more complex than a single form; but *genetically* the form is more complex in that it is the later development.

Although I have limited the discussion so far to the question of *form* discrimination, the same comments apply *mutatis mutandum* to the problem of *size* discrimination, although here I should be willing to grant that *a priori* the dependence upon the background of projection might be less than was the case with form. All experiments upon form and size discrimination that I remember having seen have neglected this factor. Controls must be used which introduce differently shaped tunnels. It is only after such experimentation that the present hypothesis—with animals and young children, "form" discrimination is always *pattern* discrimination—can be proved or disproved.[8]

[7] The subjection of children to tests with apparatus similar to that described by the authors above cited is something that should be undertaken before a truly comparative statement can be given.

[8] The writer has presented the above in theoretical form because all of his spare time is taken in experimentation along a different line. The indications are that this will be true for an indefinite period. In the interim some other investigator may see fit to carry out experiments as suggested above.

LIGHT REACTIONS OF TERRESTRIAL AMPHIPODS

THORBORG MARIE BRUNDIN

The University of California

Two figures

CONTENTS

I. INTRODUCTION

The first work in the study of light responses of Amphipods was done in the summer of 1903, by Dr. S. J. Holmes, at Wood's Hole, Massachusetts. It consisted of a number of experiments upon aquatic and terrestrial amphipods under various influences which were designed to find some clue to the mechanism of the phototactic response, and the cause of reversal in the sense of phototaxis.

The results set forth in the present paper were obtained through experiments carried on along similar lines as those of Professor Holmes, with two species of terrestrial amphipods of the Pacific coast. The work was carried on in the Zoological Laboratory of the University of California, under the direction of Professor Holmes, to whom I am indebted for many valuable suggestions and kind criticisms.

II. HABITS AND GENERAL DESCRIPTION

Orchestia pugettensis corresponds closely in appearance and habits with the *Talorchestia longicornis* of the east coast, which was experimented on by Holmes, and described in a monograph on "The Beach Flea" by Miss Smallwood. Both forms burrow in the moist sand above high water mark, are of pale grayish color and have long antennae. *Talorchestia longicornis* is strongly positive to light, and specimens will quickly congregate around a lantern set on the shore at night. *O. pugettensis*, under normal conditions, is strongly positive in the laboratory, and would no doubt act in the same manner.

Specimens were collected on the beach south of the Cliff House, San Francisco, during the months of January, February and March. In the dry sand the burrows were often from six to eight inches deep, while in the moist sand they were usually not more than three or four inches from the surface. The large specimens lie curled up and motionless, and remain so for a few seconds, sometimes half a minute, after being taken out of the sand. The smaller ones are more active and seem aroused by the disturbance of the moving sand about them. Most of the Orchestias are easily caught as they crawl out of the up-turned sand. On account of their color and stillness when first dug up, they readily escape the eye, and would get away if they burrowed down instead of coming to the surface. They run quickly over the sandpile out to the shore, where they begin to burrow, usually in depressions in the sand or against bits of wood or other objects. They apparently run in the direction of dark objects. I have often made individuals follow my foot in various directions, and burrow against the side of it.

O. traskiana were collected on a small beach at Alameda. They live under wet seaweed and collections of rubbish, a little above the high water line. Here they are found in great numbers during the day. When the grass or rubbish is lifted, they drop quickly to the ground and glide under cover, always away from the direction of the light. When unable to escape this way, they hop rapidly over the sand and hide under objects they come in contact with. In habits and reactions the species is similar to the eastern *O. agilis* upon which Dr. Holmes worked.

In order to find some connection between the habits of life of the two species and their modes of response to light and other stimuli under varying conditions, it might be well to define their chief differences, both in structure and in ways of life.

First: Differences in habitat.—*O. pugettensis* lives in the sand, burrows, and probably has little or no light during the day. *O. traskiana* lives under seaweed, seldom burrows in its native habitat, though it does burrow in confinement when it has nothing but sand to live in. It lives in a region of greater moisture than that of *O. pugettensis*.

Second: Differences in general structure.—*O. pugettensis* is about two or two and a half times as large as the adult male

O. traskiana, has a stout, round body, long antennae and strong, thick appendages.

O. traskiana is slender and delicate in limbs and antennae, has smaller eyes, and has a slender, compressed body. It is not so active as *O. pugettensis* and not at all built for burrowing. The compressed body allows it to glide quickly underneath its cover, and its color harmonizes with its surroundings, just as the color of *O. pugettensis* tones in with that of the sand in which it lives. It does not run to the extent that the *O. pugettensis* does, probably because of its narrow body and comparatively slender legs.

Third: Difference in power of withstanding dryness.—Since *O. pugettensis* lives in a comparatively dryer environment it is able to endure dryness to a greater degree than *O. traskiana*. In the dark room with a very strong light, *O. traskiana* is unable to walk after about thirty-five minutes' exposure to the air. I have not timed *O. pugettensis*, but it has often been running about an open dish for over an hour without showing signs of exhaustion.

III. PHOTOTAXIS IN *ORCHESTIA PUGETTENSIS*

When *O. pugettensis* is taken out of a sand-jar which has been standing in the window in ordinary daylight, and exposed to a strong light in the dark room, it is positively phototactic at once. Sometimes very large individuals are indefinite in their reactions for a short time, but usually they go toward the light without a moment's hesitation, whisking their long antennae at first, but later betraying but one impulse—that of getting to the light.

Effect of protracted darkness.—A twenty-four hour confinement in complete darkness does not ordinarily affect the light reactions of *O. pugettensis*. After forty-eight hours, there may be a slight negativity in some cases. I have noticed, however that after specimens have been kept in the dark-room for four or five days with intervals of one or two hours exposure to light every twenty-four hours, negative reactions take place from two minutes to seven minutes, when they are exposed to strong light. (Two minutes represents the average time of

negativity of the smallest individuals, and seven minutes represents that of the largest.)

Specimens are kept in covered glass dishes with some filter paper moistened with sea water. I do not think that the moist paper has to do with the negative reactions. I have kept two sets of *O. pugettensis* in the dark for forty-eight hours, one set in dripping wet paper and the other in a very small amount of moisture. When brought to the light, they both were positive at once.

Effect of temperature.—The most influential factor in the reversal of the sense of phototaxis of *O. pugettensis* is temperature. I put one set of about a dozen specimens on ice for twenty-four hours, and placed one set in room temperature for the same length of time, keeping both in the dark. When exposed to a light of thirty-two candle power, those kept in the room were positive in one-half minute, and those kept on ice were positive in two minutes, but remained sluggish for five minutes. Those kept in the room had been exposed to darkness for five days, hence the one-half minute's negativity. (The above reaction time denotes that *all* the specimens were positive in that time.)

Effect of blackening one eye.—*O. pugettensis* always makes circus movements toward the normal eye. This reaction is common in most of the positive forms on which the experiment has been tried. Holmes found it to be true in positive specimens of Ranatra, Talorchestia, and *O. agilis.*

When the specimen is picked up repeatedly and started from a certain point in a position directly facing the light, one notices after several trials, a gradual diminution of the curve and a growing tendency to travel to the light in a more or less direct course. Very often it started out in a straight line toward the light, but it can never keep the path straight all the way. If it begins to veer when halfway from the light, it will sometimes stop, turn until it faces the light and then travel on. The same interesting behavior was observed by Holmes in his work on Ranatra.

Effect of contact.—The inhibition of the light response by thigmotaxis depends upon the character of the contact stimulus. When specimens are shaken so that they roll about the

dish, they will feign death for a fraction of a second or longer. When they emerge from the death feint they respond to the light in exactly the same manner as before the disturbance.

A drop of water in the dish will often produce a disregard for the light. The amphipod will stop as soon as it strikes the moisture and remain in it. This behavior is more common, however, in *O. traskiana*.

Moist sand or moist filter paper will take the most active specimens from their ambitious attempts to reach the light. When at the height of their activity they may run over the sand a dozen times before they begin to burrow. The depth to which they burrow is determined by the light, as is evident from their behavior in the burrows. I put some moist sand to the depth of one and a half inches in a corner of the dish containing about a dozen strongly positive specimens of *O. pugettensis*. When I held the light so that it penetrated the burrows, there was an immediate restlessness, attempts to dig deeper and a thrusting out of long antennae. After many attempts to find shelter from the light, they would emerge head first and begin a new burrow at once, or they would run about the dish for a time in search of a suitable place to dig. Under these conditions they are generally indifferent to light.

When the light is thrown upon *O. pugettensis* under cover of moist filter paper, they become very restless and uncomfortable, and seem divided between an impulse to seek protection from the light and an impulse to go toward it. They will turn away from the light only to face it again, as if fascinated and pained at the same time. Sometimes when the light is thrown on them suddenly, they seem to be thrown back, and recoil as if from a blow. Often they cling to the filter paper and face the light stoically for some minutes. After a period of these reactions, the power of the light stimulus loses its effect temporarily, and the specimen is able to move away from it into the folds of the paper.

IV. PHOTOTAXIS IN *ORCHESTIA TRASKIANA*

O. traskiana shows so much variation and individuality in the time and manner of reacting to light, that it is difficult to lay down rules in this regard.

General reactions.—The following points may be taken to distinguish their general behavior: *First:* The smaller individuals usually become positive to light in a markedly shorter time than the larger ones. *Second:* Cold, moisture and quiet retards positive phototaxis, while heat, dryness and activity hastens it. *Third:* Contact stimuli, except in the form of moisture, do not inhibit nor reverse the phototaxis of positive specimens. *Fourth:* Positive specimens will travel tow rd the light while lying on their sides pressed between plates of glass. *Fifth:* Positive specimens with one eye blackened over, are just as likely to perform circus movements away from the normal eye as towards it.

O. traskiana is ordinarily negative to light when it is first exposed to it. The length of time during which it is negative is determined by the amount of light, warmth, moisture and activity it has had previous to being exposed to strong light. Specimens taken from moist, cold sand or seaweed become positively phototactic in from fifteen to twenty minutes. In giving the time length of reactions, I set the criterion at the point when all or nearly all specimens have experienced the change of response. In many lots of specimens, there might be one or two out of a dozen or one out of six that would still remain negative or positive as the case might be, after all the others had reversed the response. On the other hand, several small specimens might be positive very much earlier than the rest. I have endeavored to give the figures which represent the reaction time of the majority of the specimens of a given lot.

If there are a number of individuals in a dish, they form aggregations at the negative end. They remain close together with their heads turned from the light and held down. If they are not occasionally shaken up and made to run about, they may show no signs of becoming positive to the light for an hour or more. This bunching together does not happen when there are but a few individuals in a dish, and when therefore, there is greater activity.

The negative reaction is characterized by a hurried running away from the light. After a period of going back and forth along the sides of the dish (weakly negative or indifferent specimens generally keep to the sides), they begin to run across the dish at right angles to the light. Then there maybe a crossing

obliquely in the direction of the light, and finally the direct positive response begins. The first positive reactions are marked by a wavering, hurried, excited manner. The wavering then disappears, the path to the light becomes definite and the creatures become more and more excited until they begin to leap to the light, and try frantically to get to it through the side of the dish. This state of great activity lasts some time, and finally through exhaustion, they become indifferent to the stimulus, and some specimens show a weak negativity.

Reaction time of large and small specimens.—The following table shows the number of minutes of negative response in large and small specimens taken out of the dark-room in which they had been kept for twenty-four hours. Some of these had been kept in a low temperature, hence the difference in time reactions.

NUMBER OF MINUTES OF NEGATIVE PHOTOTAXIS

Large specimens	Small specimens
4	0
$3\frac{1}{2}$	2
13	5
$1\frac{1}{2}$	0
10	5
$4\frac{1}{2}$	1
10	3
$\frac{1}{2}$	0
$4\frac{1}{2}$	2
10	0
7	$3\frac{1}{2}$
$6\frac{1}{2}$	$\frac{1}{2}$
10	4

I timed one set of a dozen large and small Orchestias on five successive days. They were kept in darkness with the same conditions of moisture, and taken out every twenty-four hours and exposed to a strong light. The following gives the time reactions of the large and small specimens:

Large	Small
13	5
10	5
10	5
10	4
$4\frac{1}{2}$	0

In a set of specimens kept on ice for twenty-four hours, and then exposed to light, the large ones remained negative for

twenty minutes, while smaller specimens became positive in eleven minutes.

Cold, moisture and inactivity tend to prolong negative phototaxis in *O. traskiana*, while heat, dryness and a state of activity decreases the duration of the negative response.

On March 29th, three sets of specimens were put away in the dark under conditions of temperature and moisture as follows:

Set   I—10 traskianas—very little moisture.
Set   II— 6   "   —very moist.
Set III—18   "   —on ice.

On April 3rd, they were exposed to the light of an electric lamp in the dark room, with the following results:

Set   I—positive immediately.
Set   II—positive in eight minutes.
Set III—one-half positive in fifteen minutes, rest positive in twenty-two minutes.

Twelve specimens kept in the dark in as dry a condition as possible for twenty-four hours, became positive, when exposed to the light, in seven minutes, while five specimens kept in a condition of great moisture for the same length of time became positive in twelve minutes.

Effect of heat.—The effect of heat upon the phototactic response is shown by the following experiment: A set of about two dozen specimens, which had been kept on ice for twenty-four hours, was divided into two lots, one of which was put back on ice, and the other put on top of the radiator. The dish was wrapped up in a dark cloth so as to exclude the light After about six or seven minutes, the set on the radiator was brought into the dark room and exposed to strong light. The specimens were found to be positive in five and one-half minutes. Those kept on ice became positive in fifteen to twenty minutes.

It seems to be the rule in regard to amphipods that high temperature causes a positive phototaxis, while low temperature brings about a negative reaction of longer duration. Holmes found that *O. agilis* became positive very quickly when the

temperature was raised in case of specimens in the water and also in the air. Even aquatic species were found to become positive when the water was heated to one hundred degrees F.

I noticed often in the course of experiments that negative specimens of traskiana were made positive in a very short time if they were disturbed and kept moving about. When a specimen began to run from the light, I would stop it with a stick or bit of cardboard and turn it toward the light. After this was repeated a number of times, sometimes only six or seven times, the most negative specimens would become positive in a fraction of the time it would take under ordinary conditions.

There are but two causes, so far as I can see, that might be responsible for this hastening of the positive response—*first*— the greater amount of light stimulus received by the eyes under the constant turning toward it, and *second*, the greater amount of activity brought about by the struggle to get away from the l'ght.

Upon the hypothesis that bodily activity, no matter how brought about, would cause a rapid positive phototaxis, I shook up some *O. traskiana* in a dish in complete darkness for about ten minutes. These specimens were part of a set that had been standing in the dark for twenty-four hours in moist filter paper. I removed the filter paper, allowed about one-half of the specimens to remain quiet in the dark, and put the other one-half in a separate dish which had been moistened, in order that conditions might be the same for the two sets. These I shook up for the length of time I have mentioned, and when exposed to the electric light they became positive in two and one-half minutes, while those which had been kept quiet became positive in thirteen minutes. I tried the experiment a few days later, shaking the specimens only five minutes. The reaction time was three minutes for those disturbed, and eight minutes for those which had been kept quiet.

Holmes has shown in his work on Ranatra that after a negative specimen had been picked up and placed at right angles to the light nine times, it became positive. He found, however, that dipping positive specimens in water would reverse the response. *O. agilis* when placed in water, would remain permanently negative, while *Talorchestia longicornis* was found by Holmes to show but a very weak and temporary negative re-

sponse under the same conditions. Miss Towle found that the negative Cypridopsis would be made positive by simply jarring the vessel in which it was kept with any solid object. When she picked up specimens with the pipette and dropped them into the water, she found the positive response growing stronger with each disturbance.

Is it the contact stimulus *per se*, or is it the state of activity or non-activity brought about by contact, that produces these changes in the phototactic response? When an organism is active, metabolic processes are going on within the body, to a greater degree than when the organism is inactive. The experiments quoted above, those performed by Holmes on the eastern amphipods, and the experiments on amphipods described in this paper, have all shown that those conditions which produce a greater activity of the creature, whether external motions of legs and appendages, or internal activity in the form of metabolism, will bring about a positive phototaxis, while those conditions which decrease body activity, such as cold, moisture, quiet and darkness, will cause negative phototaxis. Whatever internal activity might or might not be produced by dipping a Ranatra in water, externally it appeared inactive. "It (a positive specimen) was then immersed in water and laid on the table. Its movements were very sluggish and its responses to light slow. When placed at right angles to the light, it would slowly and stealthily creep away. It did this eight times in succession when the right and left sides were alternately placed toward the light. At the ninth and several subsequent trials, it went towards the light. * * * Then it was picked up and stroked, but it could not be induced to feign death, and as soon as released, it made for the light * * *." Here the contact caused by picking up and stroking the specimen did not produce negative responses.

Further behavior of *O. traskiana* under conditions of contact, seems to point rather convincingly to the conclusion that contact stimulation *per se* is not of great importance in bringing about phototactic responses. Positive specimens will travel toward the light lying on their sides, pressed between two glass plates. On first thought, it would seem that contact in itself, would be sufficient to produce a state of rest and a reversal of the phototactic sense, since in its natural state, the creature's

environment is determined by the thigmotactic sense. In the
case of the two Orchestias upon which I experimented, the
contact stimulus must be enhanced by moisture, or it will call
forth no response. When I place moist filter paper in a dish,
the most positive specimens will eventually come to it, and
become immediately indifferent or negative to the light. It is
for this reason that they will still react positively to the light
even when placed in a condition of absolute contact. If I moisten
the surface of the glass plate, the creature will stop immediately,
curl up and pay no attention to the light for as long as five
minutes at a time, the length of the period of rest depending
upon the amount of moisture and the position of the specimen
with reference to the light. A specimen facing the light may
become restless and leave the moisture.

When one considers the habitat of *O. traskiana*, it does not
seem inexplicable that it should be able to travel on its side.
It usually lies curled up on its side, holding on to the seaweed
with its feet. When disturbed, it glides away on its side. *O.
pugettensis* cannot move between glass plates. The form of
its body does not allow movement in such a position. *O. tras-
kiana* has a compressed body, very fitting for its hiding places,
while *O. pugettensis* has a round body, suitable for getting into
burrows.

In performing experiments upon the behavior of *O. traskiana*
between plane surfaces, I took a plain glass plate about six
by ten inches, and pasted strips of cardboard on the sides in
order to raise it sufficiently from the table or lower surface to
allow movement of a medium sized *O. traskiana*. The lower
surface consisted of a plate of ground glass, or any hard, slightly
rough material. I left a small space of about three-fourths of
an inch in the middle of the lower six-inch side of the plate,
to be used as the point of entrance. This was made wide enough
to allow the creature free movement in pushing itself in. After
a specimen had been placed in the entrance, I sometimes blocked
it with a piece of paper so that it would be forced to go under
the plate. This was not necessary in most cases, as the creature
slipped under the plate very readily. In doing so, it went over
on its side and traveled by pushing itself by the legs against
the glass plates. Specimens set out in the direction of the
light in almost every case, but they could not always keep

going towards it in a straight path. I placed the light at different points of the plate, usually directly opposite the entrance, or on the right and left sides. The specimens would turn very definitely to the side on which the light was placed.

The formation of habits of turning was very marked. If, after the animal had traveled three or four times to the right side, the light was transferred to the left side; the animal, when placed again at the entrance, would go to the right. This happened usually once, as in succeeding trials it would turn to the light.

The behavior of *O. traskiana* between glass plates is of interest not only on account of its bearing on the importance of contact stimulation, but also in its relation to orientation. That orientation here is not a forced one, but is to a great degree under the control of the animal, seems clearly brought out in several ways.

The normal way that *O. traskiana* travels to the light is by running on its legs. When lying on its side under a glass plate, it gets to the light by pushing itself with legs and body. It will curve its body backward and forward without hesitation to keep the light in its eyes.

Besides pushing itself to the light, Orchestia will jump directly toward it, when the light is held above the dish. Jumping does not occur when the dish is illuminated from beneath. When the light is held level with the dish, excited specimens will run part of the way toward the light, and jump the rest of the distance. Usually when they jump, they turn over in the air, and land with the head away from the light. They immediately, in fact, so quickly that it is hardly noticeable, turn to the light and jump again.

O. traskiana, therefore, has a choice of three methods of reaching the light: running, pushing and jumping. Can we suppose then, that the creature is wholly forced by the equal or unequal stimulation of the light on its musculature to take a position with reference to the stimulus, and travel toward or away from it? To some degree it is. This is shown by the circus movements that occur when the stimulus is shut off from a sensitive area. The control of these circus movements in the Orchestia and in other forms, shows the beginning of the control of orientation found in the higher animals. The

mere fact that *O. traskiana* chooses its method of reaching the light tends to the conclusion reached by Holmes in his work on the phototaxis of fiddler crabs: "* * * that light is followed much as an animal pursues any other object of interest, such as prey or its mate * * *." Whatever internal condition may have arisen in these forms or how it has arisen, the more highly organized organism has some power of control within it, which is lacking in the lower forms.

Effect of blackening one eye.—*O. traskiana* shows marked individual variations of response to light when one eye is blackened. In positive specimens of Ranatra and the eastern amphipods studied by Holmes, and also in *O. pugettensis*, there were circus movements toward the normal eye when they were exposed to light. In positive specimens of *O. traskiana*, circus movements will occur as often toward the blackened eye as toward the normal eye. All specimens used for this experiment were strongly positive. There is no way to account for this variability, except that the animal might be made temporarily negative by having one of the eyes covered over. The fact, however, that as soon as the blacking is removed from the eye of one of these apparently "temporarily negative" specimens, its reaction to the light is decidedly positive, seems to throw considerable doubt upon this hypothesis.

It is interesting to observe what looks very much like a case of learning, or better perhaps, of control of the creature's movements against the influence of external conditions, in the gradual lengthening of the curve and the tendency toward traveling to the light in a straight line. I started a specimen from a point about eight inches from the light, placing it each time in a position of facing it directly. I traced its path each time. To avoid unnecessary handling, I picked up the specimen on a piece of cardboard on to which it crawled, and put it back to the starting point after each trial. The accompanying tracing of successful paths represents the average series of paths, showing the first uncontrolled circus movements, and the later more direct course of travel. The eighth and ninth trials usually show a straightening of the curved path. Holmes found the same thing occurring in Ranatra. When one eye was blackened, there was a tendency to control the veering toward the normal side, and to travel to the light in a more direct course.

The insect would stop when it began to go to the side, correct its course and travel on. *O. traskiana* and *O. pugettensi* acted in much the same manner. At times *O. traskiana* appeared to be using all its powers of control to keep from turning to the side. The body would curve to the side, but the antennae
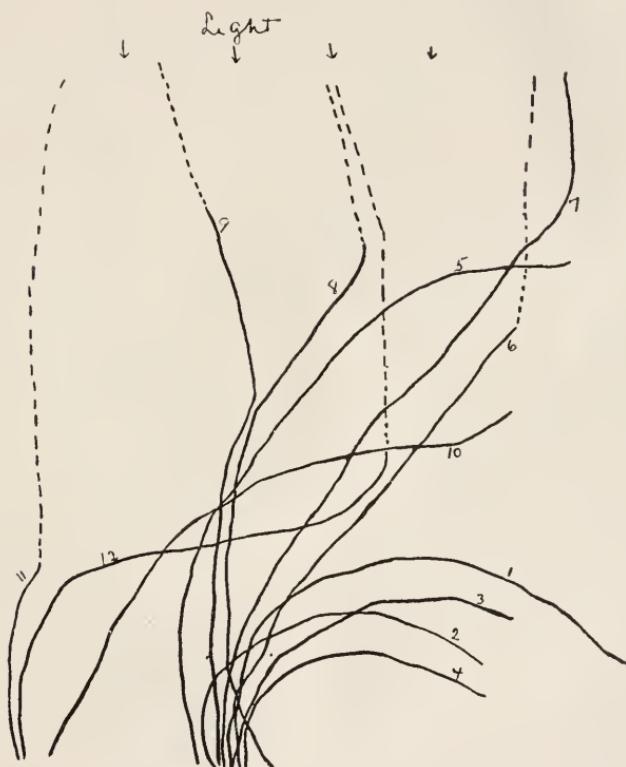
FIGURE 1.   Paths of *O. traskiana* with right eye blackened. *O. traskiana* No. 1 turning toward blackened eye. Starting point at bottom of figure. Dotted lines indicate jumping toward light. Consecutive paths are numbered.

would be extended bravely toward the light as if to help the creature to keep in the straight path. That there was effort to control its course was so visible as to be almost convincing. When specimens found themselves curving away from the light, they would stop, right their position, and go on. I did not notice that this happened more than once in one trial. The gradual straightening of the path occurred in specimens that travelled

toward the blackened eye, as well as those that travelled in a curve toward the normal eye. Holmes found that the larger Ranatras were able to correct the circus movements in a very short period of time. I noticed the same in working with Orchestia, although the fact was by no means proved, as I used
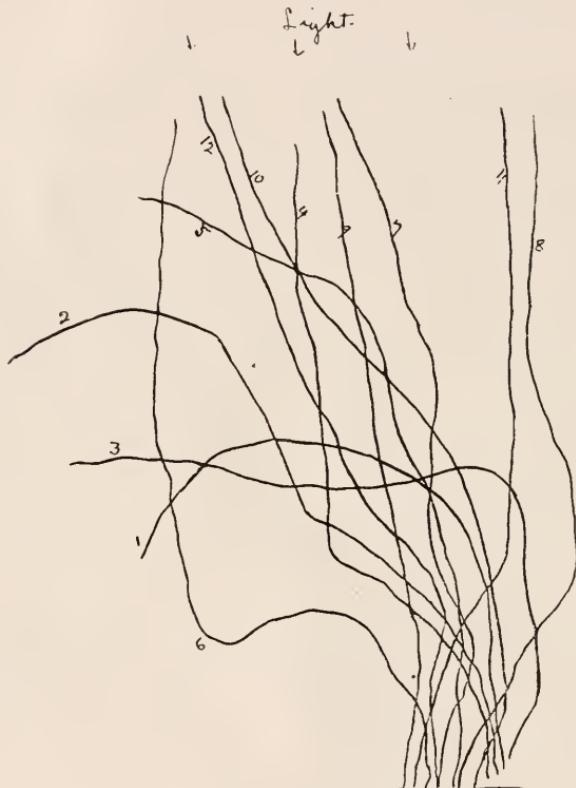
FIGURE 2. Paths of *O. traskiana* with right eye blackened. *O. traskiana* No. 2 turning toward normal eye. Starting point at bottom of figure. Consecutive paths numbered.

mainly the largest specimens for this experiment, and but few small ones.

After the blacking was removed, the animals, without exception, would turn toward or away from the previously blackened eye two or three times, before travelling directly toward the light. The same formation of habits of turning were found by Holmes in Ranatra.

Circus movements were performed when specimens with one eye blackened were made to travel under a glass plate. When lying on the right side with the right eye blackened, the curve would go toward the light. The creature seemed to be exceedingly uncomfortable in this position, and would try to turn over to the other side. When lying on the left side so that the blackened eye was above, the curve would turn to the left, i.e., toward the normal eye. This seemed to be a more comfortable position, although here too, was a slight tendency to turn over. This effort to turn from one side to the other was not manifested in normal specimens.

Effect of carbon-dioxide.—I put a dozen positive *O. traskiana* and a dozen *O. pugettensis* into a deep glass dish and filled it with CO_2. After the gas had been pouring in for about five minutes, signs of exhaustion became manifest. The specimens tended to aggregate anywhere in the dish. I constantly disturbed the aggregations by shaking the dish. Every time they were thus disturbed, they went towards the light without exception. After about twelve minutes of constant inpouring of gas, they became lifeless. The *O. pugettensis* lay on their sides or backs with their legs extended, apparently dead, while the *O. traskiana* lay on their sides, some curled up as if in a death feint, others with body and legs extended. I then shut off the gas. In about two or three minutes, they began to revive. Some went directly toward the light, others turned about a few times in one spot, before starting for the light. I tried the effect of CO_2 twice, on the same specimens within twenty-four hours. The reviving reactions on the first day were rather violent in appearance. For about two minutes they paid no attention to the light, but ran helter-skelter over one another. The largest pugettensis put his long antennae back close to his sides, hunched up his body and jumped up and down in one spot. On the second day, the reviving reactions showed none of this violent activity, but they were strongly positive at once.

It seems that carbon dioxide in certain amounts produces a stimulating effect. A. R. Moore found that Daphnia became positive to ultraviolet rays when a small amount of CO_2 was added to the water. Loeb made *Gammarus pulex*, which are normally negatively phototactic, positive by adding small

amounts of CO_2 to the water. It appears that increased amounts cause increased stimulation which finally exhausts the organism. A return to the optimum amount seems to set up again the activity that was stopped temporarily.

I did not find that carbon dioxide in itself, reversed the phototaxis of Orchestia. I let the gas flow into the dish of specimens that had been in the dark for twenty-four hours, until they were unable to move. When I brought them to the light they were negative.

V. GENERAL CONCLUSIONS

In studying the light reactions of the Amphipoda comparatively, we find that the aquatic Gammaridea* are permanently negative to light under natural conditions, while the most terrestrial forms are positive. The forms occupying a position somewhere between the aquatic and the most terrestrial are those which live on land in very moist conditions, such as the *O. agilis* and *O. traskiana*. These are positive, but have a preliminary negative reaction. Talorchestia and *O. pugettensis*, which live in the sand higher on the shore, are ordinarily positive at once to light. We find, therefore, that among the Amphipoda, the more terrestrial forms are the more positive.

It was found by the experiments performed, that the conditions which bring about the positive phototaxis, are the conditions which prevail in the environment of the more terrestrial Amphipoda. Heat and dryness favor positive reactions, while cold, moisture and quiet favor negative reactions. *O. pugettensis* lives in a dryer, warmer environment than *O. traskiana*. *O. traskiana* makes no hiding place for itself, and lives under conditions of greater cold and moisture.

The small individuals of *O. traskiana* are very active. Their periods of negative reactions are correspondingly short when compared with the larger, more sluggish specimens. Yet even these latter can be made positive to the light by enforced activity, and by dryness and heat. These factors produce metabolic processes, through which the chemical reactions which may perhaps be necessary to a certain response, take place. They may also affect the nervous system in such a way that the shock produced by a certain stimulus may be greatly increased or

---

* Holmes: Phototaxis in the Amphipoda.

reduced as the case may be, and so cause a modification of the response.

The bearing that the above considerations might have on the evolution of a species can only be set forth as a suggestion. It is difficult, however, to ignore the significance of the power of adjustment that these forms show in their choice of methods of reacting to a stimulus, and in their power to control their reactions over against the mechanical effects of a stimulus. This adjustment is shown in their behavior under a glass plate, in the method of jumping toward the light, when it is held above the creatures, and perhaps most important of all, in the controlling of the circus movements. This last mode of behavior exhibits a transition from the stage at which the creature is at the mercy of its environment, to a stage at which it is beginning to hold its own against the forces which have shaped it. The reactions of plants and many lower organisms show little or no power of choice or control over stimuli. As we proceed to the higher forms, we find this power of adjustment and control increasing, until we find the animals that have survived mainly through their mastery of the forces of the environment in which they were thrown.

BIBLIOGRAPHY

COLE, L. J. An experimental study of the image-forming power of various types
1907.   of eyes. Proc. Amer. Acad. Arts and Sci., vol. 42.
HOLMES, S. J. Phototaxis in the Amphipoda. Amer. Journ. Physiol., vol. 5, pp.
1901.   221-234.
1905.   The reactions of Ranatra to light. Journ. Comp. Neur. and Psych.,
            vol. 15, pp. 305-349.
1905.   The selection of random movements as a factor in phototaxis. Ibid.,
            vol. 15, pp. 98-112.
1912.   The tropisms and their relation to more complex modes of behavior.
            Bull. Wisconsin Nat. Hist. Soc., vol. 10, pp. 13-23.
JACKSON, H. H. T. The control of phototactic reactions of Hyalella by chemi-
1910.   cals. Jour. Comp. Neur. and Psych., vol. 20, pp. 259-263.
LOEB, J. Der Heliotropismus der Thiere und seine Uebereinstimmung mit dem
1889.   Heliotropismus der Pflanzen. Würzburg.
1900.   Comparative Physiology of the Brain and Comparative Psychology.
            New York, pp. v+303.
1904.   The control of heliotropic reactions in fresh-water crustaceans by
            chemicals, especially CO_2. Univ. of Calif. Pub. in Physiol., vol. 2,
            pp. 1-3.
MAST, S. O. Light and the behavior of organisms. New York, pp. 1-378.
1911.
MOORE, A. R. Negative phototropism in Diaptomus by means of strychnine.
1912.   Univ. of Calif. Pub. in Physiol., vol. 4, pp. 185-186.
1912.   Concerning negative phototropism in Daphnia pulex. Journ. Exp.
            Zool., vol. 13, pp. 573-575.

RILEY, C. F. CURTIS. Observations on the ecology of dragon-fly nymphs: rela-
     1912.   tions to light and contact. Ann. Ent. Soc. Amer., vol. 5, pp. 273-
               291.
SMALLWOOD, MABEL E. The beach-flea: Talorchestia longicornis. Cold Spring
     1903.   Harbor Mon., 1-6, pp. 3-27, 3 pl., 3 figs. in text.
     1905. The salt-marsh amphipod: Orchestia palustris. Ibid., pp. 3-21, 2
               pl., 1 map.
WODSEDALEK, J. E. The formation of associations in the May-fly nymphs *Hepta-
     1912.   genia interpunctata* (Say). Jour. Animal Behavior, vol. 2, pp. 1-19.

THE HABITS OF *EUMENES BELFRAGEI*, CRESS.[1]

CARL HARTMAN

The University of Texas

Seven figures

The present paper is a record of the habits of *Eumenes belfragei*, Cress., one of the mason wasps of the family Eumenidae. The members of the genus Eumenes have long been subjects of interest, chiefly perhaps for esthetic reasons, since this wasp is an expert mason, building a neat nest in the shape of a water bottle on the stems of herbs and shrubs. The nest is symmetrical and graceful in outline and is provided with a neck and a rim around the mouth. The outer surface is, moreover, decorated with "sculpturings." Within this nest the wasp lays an egg and then stores the nest with a score or more of small caterpillars, after which she plugs up the mouth of the cell and goes away to repeat the performance elsewhere.

Eumenes is solitary in its habits and in this respect resembles the Sphecina or digger-wasps, with which group most solitary wasps are classed. On morphological grounds, however, especially because of the plaited wings, Eumenes is allied to the social wasps and is classed with these under the superfamily Vespina. A general classification of the stinging wasps on the basis of habit is given in the following outline for the further orientation of the reader.

I. Vespina (True wasps.)	1. Social wasps (Vespidae)	a. Mud plugs in ready made cavities. (E.g., Odynerus, sp.)
	2. Solitary wasps. (Few digging; mostly mud-working: Eumenidae.)	b. Mud nests. (E.g., Eumenes, Odynerus, sp.)
II. Sphecina (All solitary.)	1. Digging wasps. (Nests dug in the ground.)	a. Mud plugs in ready-made cavities. (E.g., Trypoxylon.)
	2. Mud-working wasps.	b. Mud nests. (E.g., Pelopaeus, Agenia.)

The outline shows that the habit of making mud nests has arisen in different groups of wasps. Indeed the habit of work-

ing in mud is widely distributed among insects: wasps, bees, ants and termites. In fact, certain mining bees (e.g., *Emphor bombiformis*, Cress.), have two habits which, so far as the writer is aware, are not both present in any one wasp, namely, the habit of digging the nest in the ground and that of using mud for partitioning and plugging up the nest.

The following account describes observations made on Aug. 11th, 12th and 13th at Huntsville, Walker County, Texas. The account concerns two wasps which worked upon their nests about the same time. These individuals will be referred to as No. I and No. II. Wasp No. I was first discovered among a dozen or more Pelopaei which were gathering pellets of mud at a small puddle of water formed from the drippings of an
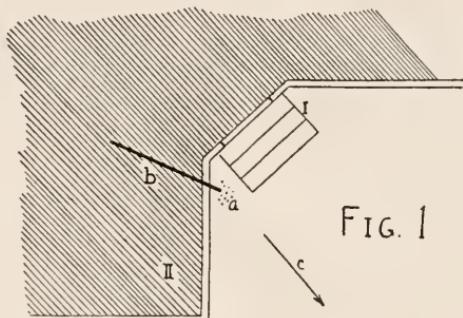
Fig. 1

ice box. Eumenes had been drinking water; from the water it flew to a lump of clay from which it gnawed a pellet of moistened dirt and then proceeded with the pellet to the nest a few feet away. Fig. 1 represents the location of the two nests which the writer observed the wasps build and store. The shaded portion is the veranda under the floor of which the observer crouched to escape the scorching rays of an August sun. Nest No. I was attached to a culm of Bermuda grass (*Cynodon dactylon*) under the steps (I, fig. 1); nest No. II was similarly placed under the veranda at II. The letter *a* represents the puddle of water from the drain-pipe *b*. The building of the second nest will be described, as every step in the work of the second wasp was observed, from the first reconnoitre for a suitable nidus to the closing of the nest. Occasional reference will be made to the work of wasp No. I.

Wasp No. II appeared on the scene soon after No. I was discovered. The former at first followed no definite course, but flew about from place to place, examining stems of grass and other objects, apparently looking for a suitable situation for the nest. Soon it seemed satisfied with a grass stem in the center of a clump of grass several feet back from the edge of the veranda.

That the reconnaisance was now over was apparent from the wasp's change of manner. It flew about over the clay soil, stopping at many different clods. No suitable material seemed to be found near at hand, for it flew off to the garden (direction of arrow *C*, Fig. 1) and remained away several minutes. It then returned with a pellet of wet clay, 3 mm. in diameter, carried with the mandibles. The wasp made its way to the blade of grass last examined and applied the first load of mud in and about the axil of the grass blade. Thus this artist of nature began its two hours' task. Twenty-six loads were required to complete the nest. The following table gives the time of return with each load and the number of minutes the wasp was absent .each time:

Load	1	2	3	4	5	6	7	8	9
Time	1:49	1:55	2:08	2:14	2:20	2:30	2:35	2:39	2:51
Minutes absent	..	6	8	6	6	(10)	5	4	(12)
Load	10	11	12	13	14	15	16	17	18
Time	3:08	3:17	3:20	3:23	3:27	3:41	3:45	3:48	3:57
Minutes absent	7	(9)	3	3	4	(14)	4	3	(9)
Load	19	20	21	22	23	24	25	26	27
Time	4:00	4:04	4:07	4:10	4:19	4:23	4:27	4:30	4:35
Minutes absent	3	4	3	3	(9)	4	4	3	5*

* Returned to lay the egg on this visit.

Eumenes differs from the common Pelopaeus in the manner of securing her building material. The latter uses the mud already present in water-soaked soil and merely rolls up a ball with the mandibles and fore-feet. Eumenes selects a hard place, often a well trodden path, and secures the mud by first softening it with water from its crop. The writer has also observed this habit to obtain with Odynerus, with Agenia, and with the mining bee Emphor.

Our wasp No. II secured mud from a spot of some fifteen square inches in area in a well-beaten path at the near edge of the garden some twenty feet away. Only every fourth or fifth trip was taken out of sight beyond the garden more than one hundred and fifty feet distant. Presumably it went for a drink of water on these longer trips, for it invariably returned with a pellet of mud without stopping at the nearer spot. Each long trip was followed by three or four short ones to the nearby quarrying place in the pathway of the garden. An inspection of the table above shows that the wasp returned on the trips Nos. 6, 9, 11, 15, 18 and 23 after an absence of nine to fourteen minutes. These trips were made beyond the garden; the other trips, consuming less time, were made only to the nearer source of supplies. Twenty loads were secured from the spot just inside the garden leaving twenty small pits that could easily be counted after the wasp had completed its task. The longer time required for the wasp to return to the nest on the first five trips might be ascribed to the unfamiliarity with the way in and out among the objects in the approach to the nest.

It was commendable economy for the wasp to select a reasonably close spot for quarrying between drinks. It is, however, not complimentary either to the wasp's intelligence or to its power of adaptation that she flew many yards to secure water when there was a puddle within a few feet, which was, indeed, not disdained by wasp No. I. The latter economized effort in that it had water, dirt and the nesting place within the radius of three feet. It is, of course, possible that wasp No. II on this occasion simply returned for water to the same place whence it had secured water for nests previously built.

It is worthy of note that wasp No. I secured all the dirt to build its nest from a single clod of clay, and that twenty-four hours later (!), when ready to close the nest with a mud plug, it drank deeply of water and flew back to the *same* clod of dirt, whence came the rest of the building material, and secured there the last bit of mud needed to make its offspring safe. The "memory" of the situation of the clod of clay persisted, therefore, for a night and a day, although the daytime intervening was filled with such strenuous activities as the capture, stinging, and storing of a score of caterpillars, not to speak of the laying of the egg.

The work of nest building proceeds without hesitation. The mud brought at each load is applied immediately on the arrival of the wasp. The first few loads are plastered around the grass stem and blades and serve to anchor the prospective nest to its foundation. The sixth load completes a flat circular disc, vertical in position, firmly fixed to the grass. The seventh, ninth, eighth and tenth loads are applied respectively to the upper, lower and lateral edges of the disc and then pulled out. There is now the first indication of the future cavity of the nest. Loads eleven, twelve and thirteen form another ring of mud, each application lapping over the individual portions previously applied, as is the rule in the nests of the Pelopaei. Perhaps this avoidance of coincident joints adds to the strength of the nest.

The upper portion of the nest grows faster than the lower until the point is reached in the upper portion where the neck of the " bottle " is to be; then the lower edge of the now rapidly diminishing opening is built up until the opening is only 3 or 4 mm. in diameter. The neck and the rim are now put on with the last three loads of mud. The neck has a lumen 2 mm. in diameter.

The wasp's manner of working is of interest. The work of plastering on and smoothing down the mud is performed with the mandibles and the forelegs, the other legs being used only to hold on. The pellet of mud is placed on the desired spot where it adheres (fig. 2). It is then rolled with the forelegs and mashed with the mandibles, the motion continuing in one direction as long as the quantity of mud will allow. Like all movements of this wasp this spreading movement is perfectly steady and devoid of any jerky motion characteristic of the Sphecina.

The mass of mud is now in the shape of a ribbon on the edge of the wall of the cell. The mud must next be pulled up so as to thin it out to the normal thickness of the wasp's nest. This is done by squeezing the mud between the head (mandibles) and the forefeet, the feet on the *outside* and the head on the *inside* of the nest (figs. 3 and 4). No exception to this rule has been noted. Thus, to make a homely comparison, if the human hand were to perform this task, the mud would be molded between the thumb and the index finger.

In this work of smoothing each load of mud the front tarsi meet at an angle approximating ninety degrees. Thus it happens that at the apex of the angle, that is, around the claws of the feet, more mud generally gathers than at other points. Frequently the work is left before this lump is perfectly smoothed out and as a result a permanent papilla or tubercle remains
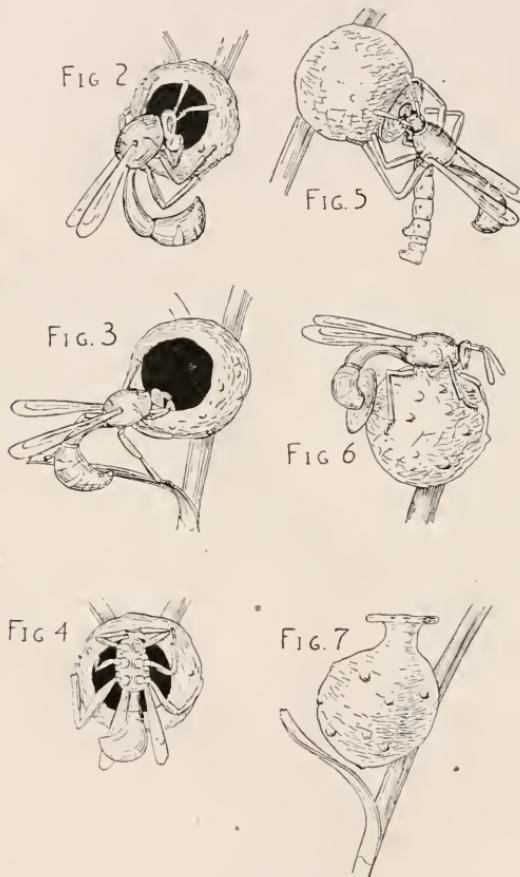
when the mud hardens. As the wasp works with the feet on the outside of the nest, the tubercles appear as the "decorative features," the "sculpturings" of the nest, to which various authors have made reference (fig. 7). On the average about fifteen tubercles appear on one nest. A little less than half of the loads are, therefore, smoothed off perfectly, leaving no tubercle.

The neck of the bottle is made quickly and with remarkable deftness. A pellet of mud is applied to the edge of the hole from which the neck is to be built up. Then, with the mandibles on the inside and the tarsi on the outside of the nest, as before, the neck is drawn up smooth and perfectly round, the wasp imitating the effect of the potter's wheel *by turning herself round and round* as she draws the mud out into a tube. The result is that the neck is a perfect cylinder. The rim or flange is similarly made. The twenty-fourth load was placed on the edge of the hole and pulled up to form the base of the neck; the twenty-fifth load formed the remainder of the neck and part of the rim; the twenty-sixth load completed the rim.

The writer has wondered what the functions of the neck and the rim of the cell could be. Neither is of use to the offspring, for the next generation makes exit from the nest by gnawing a circular hole through the wall. If of use at all, these structures must serve the adult wasp in the process of laying the egg, storing the nest or plugging up the entrance. The rim may serve the wasp to hold on when it pushes the caterpillars into the nest, and, indeed, may serve as a kind of funnel. It would seem, too, that this entrance is more effectively closed with mud when the whole work is completed. The writer is inclined to believe, however, that the neck enables the wasp to press more caterpillars into the nest without their falling out than would be possible without it.

After the rim was completed the wasp indicated the fact that the nest building was over by flying away to a nearby shrub and leisurely cleaning her legs and antennae. In a few moments, however, she was back to the nest, climbed upon it and protruded the abdomen as far as possible into the neck of the nest (fig. 6). In this position she remained six minutes. The egg was laid at this time. The egg is thus laid before the nest is stored, as is true of all Eumenidae and probably of some Sphecina, e.g., Monedula and Bembex, though the latter feed their growing larvae from day to day.

As stated above, the neck of the nest facilitates the pushing in of the caterpillars. The capacity of the nest is surprising. When the wasp brought the first caterpillar, the writer estimated that the nest would hold seven or eight. After about fifteen caterpillars had been brought in the observer actually

examined the nest to see if the bottom had not fallen out! But caterpillars continued to be pushed in until the feat seemed almost uncanny. Nest No. I held twenty-four; nest No. II, twenty caterpillars.

Following are the times that wasp No. I returned with her twenty caterpillars—Aug. 12th: 9:30, 9:37, 10:00, 10:50, 11:10, 11:17, 11:35, 1:10, 2:15, 3:10, 3:26; Aug. 13th: 8:15, 8:40, 8:48, 9:07, 9:30, 10:20, 10:36, 10:46, 11:00. The variable time required to obtain the prey (6 to 65 minutes) indicates the large part that chance plays in the finding of the prey.

The caterpillars stored by Eumenes belfragei are Geometrids, the largest of which exactly fit into the lumen of the neck (fig. 5). The wasp carries the caterpillar with the mandibles and all the legs, flying with it in and out among the grass blades all the way to the nest.

In flight, the body of Eumenes is held horizontal. So smooth are the movements that the wasp may be said to sail along, turning to right and to left to avoid obstructions as though guided by a rudder. The flight of the wasp is extremely graceful and one that is characteristic of the Eumenidae. To the thorough observer the wasp's general manner of movement is as definite a character of the group as any morphological character.

It should also be stated that the wasp did not always fly in the same direction when starting out for the hunting grounds, for she passed around the house to the north as well as to the west.

Nest No. II was opened Aug. 16, when the larva had devoured all the twenty-four caterpillars stored. The larva soon spun a cocoon of white fibers, which remained white permanently. On Sept. 4, twenty-four days after the egg was laid, an adult male emerged.

From nest No. I was reared a parasite (Microdus (Crassi microdus) sp. nov.).

The determination of Eumenes was made by Mr. S. A. Rower; of the parasite by Mr. H. L. Viereck, to each of whom the writer's thanks are due.

REPRODUCTION OF INARTICULATE SOUNDS IN THE PARROT[1]

K. S. LASHLEY

During the past winter I had a brief opportunity to observe and experiment upon an Amazon parrot which shows a rather exceptional responsiveness to the actions of his human companions. The experiments are incomplete and in many ways unsatisfactory but as it is not probable that further observations can be made for some time it seems best to record such data as are at hand, since they offer a rather striking example of the extent to which circular imitation may be developed in these birds.

The bird studied, a large Amazon (Chrysotis sp.) was imported in 1892 when about six months old, and since that time has been kept as a pet in a small family. No regular method of training has ever been employed and no records of his behavior have been kept. When about nine months old he began to talk and during the past ten years his vocabulary has varied from 50 to 100 distinctly articulated words. At present he speaks some 60 words singly and combined in various phrases.

Besides these words, he gives a number of inarticulate sounds which are distinguishable from the instinctive notes of his species. He "sings, whistles, barks, mews, cackles, coughs" and gabbles an endless jargon of meaningless syllables with rising and falling inflections, reproducing the sound of a man's voice heard indistinctly. These sounds are sometimes given spontaneously but are more often called forth by some stimulus; visual, as when the bird mews at the sight of a cat; or, more frequently, auditory, as when he repeats the cat's mewing. In this they differ from all of his articulate sounds which are almost never given in repetition of auditory stimulation. The inarticulate sounds thus offer the best material for experiment, both because they are given in response to auditory stimulation, and because their wide qualitative range lessens the danger of false interpretation by the observer.

[1] From the Psychological Laboratory of the Johns Hopkins University.

361

The older literature of animal psychology abounds with anec-
dotes designed to display the intelligence of the parrots, but
there has been no experimental study of the birds and nothing
is known of the manner in which they learn to speak; whether
by direct imitation, by the gradual imitative modification of
instinctive notes or by chance combinations of instinctive notes
which, meeting the approval of the trainer, are rewarded and
so "set" in memory. Certain preliminary questions arise before
it is possible to attack the problem of the method of learning.
What is the instinctive equipment of the bird, his notes, his
ability to distinguish pitch and timbre, etc.? To what extent
does auditory stimulation modify his behavior? What is the
rôle of imitation in the reactions of the trained bird? What is
the motive for the reproduction of non-instinctive sounds?

The following observations suggest answers to these ques-
tions but, because of their limited scope, can not be looked
upon as at all conclusive.   •

The method of experiment used was very simple. The bird
was perched upon the back of a chair and various sounds were
made, his first response to each alone being considered. At
the beginning of each series of tests a melody was played to
get him to respond more readily. In experiment 3 the pitch
of stimulus and response were determined by the help of a piano.

EXPERIMENT 1. TIMBRE

Whistling and singing tones were given in irregular order as
stimuli and the bird's first response was recorded. The results
may be summarized as follows:

30 whistling tones, produced by the lips and by a small metal
whistle, were in every case followed by a distinct whistling tone
in response.

31 singing tones from violin, cello, piano and voice were
followed by singing tones in 29 cases and twice by whistling.
Other tests, given with another purpose, confirm these results
and extend the observations to more than 100 cases.

It is unfortunate that control experiments in which the ex-
perimenter remained hidden from the bird could not be carried
out. Before the first tests were undertaken, while I was talking
in a room where the bird could not see me, he began to chatter
in a low pitched tone and I induced him to whistle, sing and

speak in response to similar sounds. Believing that this result could be repeated easily, I made no records at this time. Later I was unable to get any response at all when the bird could not see me. However, in view of the fact that the bird was hardly familiar with the piano, not at all with the violin or cello, and had learned to sing by hearing the human voice only, the lack of control experiments does not seem to invalidate the results.

EXPERIMENT 2. TIMBRE

With the purpose of bringing out a somewhat wider range of sounds the following experiment was undertaken. Whistling, coughing, smacking of the lips, whispering and guttural speech were used as stimuli, repeated in irregular order. The results were:—

Stimulus	Times given	Response	Times given
Guttural speech........	10	Guttural muttering...	10
Whistling.............	10	Whistling............	10
Whispering...........	10	Whispering..........	10
Cough................	10	Cough...............	10
Smacking of lips.......	5	A similar sound......	4 }
		Whispering..........	1 }

Control experiments are again lacking but I did succeed in obtaining the responses while my hand was so held that the bird could not see the movements of my lips in making the sounds. The results of this and the preceding experiment seem to furnish sufficient evidence that the responses were given upon the basis of sound and that the bird is able to distinguish clangs and musical tones through the range of pitch and timbre employed. He does not reproduce the timbre of the sounds with absolute accuracy (there is no difference between his responses to the piano, violin and voice) and, while this is probably due to the limitations of his vocal apparatus, it makes it somewhat more difficult to state with certainty that the responses are imitative. The reproduction of pitch offers a more conclusive test of this, since it is less likely to have been learned by any chance system of reward or punishment.

EXPERIMENT 3. PITCH

The bird's singing register is about one octave extending upward from C^{256}. Notes within this interval were sounded

upon the piano and violin. The bird sang readily enough in response to these sounds but did not reproduce their pitch. More frequently the response consisted of several notes, often with the addition of words as, "Oh, little birdie, Oh," sung with five changes in pitch. This is in accord with his manner of singing alone and it was found so difficult to obtain single notes that singing tones were soon abandoned.

Whistling tones were next used as stimuli. The bird's whistling register is somewhat more extensive than his singing one. It extends upward from F^{384} for about two octaves. The response to a single whistling tone was usually a single note also, but sometimes several notes were sounded. In the latter case the first note only was compared with the stimulus.

The results of this experiment have been combined in a correlation table, printed below. In this table the intervals represented are each two half tones on the chromatic scale, beginning with F^{384}.

Responses	Stimuli													
	1	2	3	4	5	6	7	8	9	10	11	12	13	.
3	1			1				1						3
4				1					1					2
5														
6					1				1					2
7							1							1
8			1					1						2
9					3	2	1		6	1			1	14
10			1			1			1					3
11								2			2			4
12												2	1	3
13							1		1				5	7
	1		2	2	4	3	3	4	10	1	2	2	7	41

TABLE OF CORRELATION IN PITCH BETWEEN STIMULUS AND RESPONSE

The coefficient of correlation obtained from this table is 0.658 ±.059. This expresses a degree of likeness between stimulus tone and response that is far too great to have been due to chance alone, and indicates that the bird actually tends to reproduce the pitch of the stimulus.

EXPERIMENT 4. MELODY

A number of attempts were made to get the bird to reproduce several successive notes. Stimulation by short melodies usually

called forth a melody in response but one having no resemblance to the original stimulus. There was never any evidence of the imitation of two or more successive tones.

MELODY AND INTENSITY

At times I had great difficulty in obtaining responses to single notes although the bird would sing quite readily when a melody was played. In accompanying a melody his voice rises and falls with many marked changes in pitch but does not follow the melody closely. He is affected to a marked extent by the intensity and rapidity of the music. A slow tempo will rarely induce a reaction; rapid playing, on the contrary, will arouse him to a condition of high excitement in which his movements become rapid, his crest is erected and his tail spread. Changes in intensity have a like effect.

THE IMPULSE TO IMITATE SOUNDS

There is no experimental evidence bearing upon the motive which impels the parrots to imitate sounds foreign to their species. The bird described in this note was in a constant stage of rage during the experiments, attacking me frequently and once striking at my face with such violence as to throw himself from the chair. A young bird of the same species which I now have in my possession persists in giving almost his entire repertoire of instinctive notes whenever he hears any musical sounds, and this in spite of severe and repeated punishment. These facts suggest that reward is not an important factor in the parrot's reproduction of sounds. The whole attitude of the bird in reacting suggests the action of an instinct for competition. His movements during reaction frequently suggest the courting activities of other birds and it seems not improbable that the principal motive for the parrot's reproduction of sounds is to be sought in a perverted form of sex rivalry. However, much more extensive experiments with observations upon the birds under natural conditions will be necessary to settle this question.

SUMMARY

The data presented indicate that the parrot is able to distinguish sounds of widely different pitch and timbre and to reproduce them.

The bird's capacity for circular imitation may be developed to a surprising extent by the conditions of captivity.

The impulse to imitate various sounds is hard to determine. It is connected very intimately in all probability with the sex life of the animal.

SOME EXPERIMENTS ON THE METHOD OF ORIENTATION TO LIGHT

S. J. HOLMES AND K. W. McGRAW

One of the questions raised in recent years concerning the orientation of animals to light is whether light acts as a constant stimulus or stimulates mainly through its fluctuations of intensity. We may conceivably explain the orientation of an insect, for instance, by the supposition that when there is a deviation from the line of orientation to the left and a diminution of the light entering the left eye (or an increase of light entering the right one) the change in light intensity produces a reaction that turns the insect to the right. Deviations toward the right of the direction of the rays being responded to by a turn toward the left the insect would automatically keep in a position of orientation. We know that changes in the intensity of light, whether an increase or a decrease, may act as a stimulus, especially if the changes are sudden. In many animals it is not so much the intensity of the light that induces a response as the shock of transition from one intensity to another. Is it possible to explain orientation in general as the result of such responses?

Some years ago it was found by one of the writers (Holmes,[1] '05) that Ranatras with one eye blackened over were sometimes able to go toward the light in a nearly straight line. While there was a tendency to turn toward the normal eye, there were counter movements which held this tendency in check. It was pointed out that "Were the insect so constituted as to respond to an increase of light entering the left eye by a turn to the left and to a decrease of light by a turn to the right, we can understand how, when once pointed towards the light, a straight course might be preserved. If the insect turned towards the right there would be an increase of light entering the left eye which we might suppose stimulates the insect to turn in the opposite direction. Deviations to the left would cause a diminution of light entering the left eye, which we might sup-

---

[1] Holmes, S. J. The reactions of Ranatra to light. Jour. Comp. Neur. and Psych. 1905, vol. 15, pp. 305-349.

pose acts as a stimulus to turn to the right side. The right eye may be supposed to act, *mutatis mutandis*, in a similar manner." The general upshot of the discussion was that whatever rôle the fluctuations of light intensity might play in the orientation of Ranatra they did not alone afford a satisfactory explanation of orientation, and the tentative conclusion was reached that each of the two factors mentioned "may supplement the other in such a way as to coöperate in the maintenance of a direct course towards the light."

Mast,[2] who is an opponent of the view that phototaxis is the result of light acting as a constant stimulus, is favorably disposed toward the alternative supposition which makes orientation a function of differential sensibility. In speaking of orientation in many lower forms, he says: "In many of these forms orientation is undoubtedly, and in all it is probably, a response to change of light intensity on some part of the organism. At any rate it has in no instance been demonstrated that it is, as Loeb states, 'a function of constant intensity,' that orientation to light is like orientation to an electric current."

While there are many facts that indicate that light exercises a stimulating effect on organisms quite apart from the shocks due to variations of intensity, the question as to the relative potency of the two influences mentioned, which Mast has done well to bring into greater prominence, is one that can be answered only by experiment. In the ordinary movements of animals to or from the light both these two factors are free to come into play. The natural method of attacking the problem, therefore, is to exclude one of the possible agencies, and then to observe the effect of the other alone.

To this end an apparatus was devised consisting of a jar lined below and at the sides with white paper. This was covered by a cone of the same material in the apex of which was placed an electric light. A small peep hole permitted the observation of insects placed in the jar. In several experiments the insect was placed in a small circular glass dish in the center of the enclosure. Whether the insect turned to the right or to the left in this apparatus, the amount of light entering the eyes was approximately the same. Insects with one eye blackened over were placed in the jar and stimulated to activity whenever

---

[2] Mast, S. O.   Light and the behavior of organisms.   New York.   1911.

they came to rest by tapping on the jar, or when this failed by poking them with a wire. The very slight variations in the light entering the eye in the different positions of the insect would have different effects, according to the theory of differential sensibility, depending on the position of the insect, and would not tend to produce a constant deviation of the path in any particular direction. The same may be said of the variations caused by movements out of the horizontal plane. Since the slight effects of differential sensibility would tend to neutralize one another, any uniformly directed movements may be attributed, with considerable probability, to the constant stimulating effect of the light.

Several experiments with different species of insects gave very indefinite results. Some insects would not move, or simply went to one side of the enclosure and crept around in contact with the wall; in other cases the movements were apparently at haphazard. In general where the movements were indefinite inside the enclosure they were equally so outside of it. Several beetles belonging to three different species showed a tendency to turn toward the blackened eye. Previous tests showed the beetles to be negatively phototactic and their turning to the blackened eye is what one might expect if they behaved within the enclosure as most negative forms do under ordinary conditions of unilateral stimulation. There was a considerable amount of irregular spasmodic movement, as there generally is in the phototactic activities of beetles, but their tendency to turn toward the blackened eye was sufficiently pronounced to be unmistakable.

A Jerusalem cricket, Stenopelmatus, which is negative to light was placed in the enclosure after having its left eye blackened over. When crossing from one side to the other it invariably turned to the left, and when it came in contact with the edge it continued to go around in that direction. When headed in the other direction it would go but a short distance toward the lighted side and then turn around again.

Experiments with butterflies gave results that were variable and in some respects puzzling. In one experiment a *Euvanessa antiopa* with the right eye blackened over circled toward the left directly eight out of eleven times. In the other three trials it went ahead a short distance and then to the left. In seven

subsequent trials the turns were toward the left in every case. In one experiment with a skipper butterfly with the right eye blackened there were circus movements to the right in nine out of ten trials. With another specimen of the same species there were circus movements toward the blinded side in six out of seven trials. In another specimen there were circus movements toward the blinded side in all of the six trials that were made. The cause of the turning toward the blinded side was not carefully investigated. Ordinarily this species of skipper shows a positive, although somewhat spasmodic positive phototaxis. Like some of the butterflies studied by Radl [3] and Parker [4] it shows a tendency to orient negatively when basking in strong sunlight. Possibly the circus movements of the skippers toward the blinded side may be associated with this trait of negative orientation when at rest in a strongly illuminated region. Experiments with two specimens of *Melitæa chalcedon* with the right eye blackened over showed circus movements to the left in thirty successive trials in each case. After a half-hour's interval each specimen made ten circus movements to the left.

Two specimens of the fly Tachina with one eye blackened over showed very decided circus movements toward the normal side in each of twenty-five trials. The body was held leaning over toward the normal side and the insects showed a tendency to roll over toward that side. A specimen of *Eristalis tenax* showed circus movements toward the normal side in thirty successive trials, and a tendency to lean over toward the normal side. Several other experiments with other flies gave very similar results. The tendency to hold the head and body tilted over toward the normal side is very noticeable in several species of Diptera that were previously observed in an ordinary environment. It was especially marked in a species of robber fly, Asilus, which when at rest leaned over so strongly toward that side that in its attempts at locomotion, which eventuated in the usual circus movements, it would continually fall over. The light in this case seemed to exercise a strong, continuous and almost uncontrollable effect on the tonus of the muscles.

It was observed by one of the writers that Ranatras when

[3] Radl, E. Untersuchungen über den Phototropismus des Tiere. Leipzig. 1903.
[4] Parker, G. H. Phototropism of the mourning-cloak butterfly, Vanessa antiopa Linn. Mark Anniversary Volume, pp. 453-469. 1903.

held in the hand in a fixed position often made struggles to turn toward the light. These would frequently manifest themselves by reaching toward the light with the anterior prehensile legs, and if the insect was in a position to get the feet in contact with a solid object, by pushing and pulling with the other legs also. This fact, together with the persistence for a considerable interval of certain attitudes of the head and body that were assumed in relation to the source of light, seemed to point to a fairly constant stimulating influence of the rays. However, when the insects were fastened to a glass rod and suspended in the air the legs showed no definite response to unilateral stimulation. A considerable number of phototactic insects were held near the light to find if any effect could be noticed in the attitudes of the appendages, but the results, as Radl also found in similar experiments on a number of insects, were entirely negative.

While no effect of light on the muscular tonus of the legs was manifest so long as the legs were allowed to dangle loosely in the air, it was thought that such an effect might be demonstrated if the legs were given something to act upon which could be moved without altering the position of the insect in relation to the source of light. Profiting by a suggestion from Prof. S. S. Maxwell a device of this kind was constructed consisting of a thin horizontal disk rotating on a pivot like the turntable of the microscopist. The apparatus was made very light and easy running so that even a small insect could set it in motion. By holding an insect over the disk with the head pointing either toward or away from the center, and having a light so that the rays fell upon one side of the body, the movements of the legs which would ordinarily turn the insect toward the light would simply cause the disk to rotate in the opposite direction. With the insect held steadily, the stimulus afforded by the light would naturally remain constant, and if light oriented by its constant stimulating effect we might expect the insect would keep rotating the disk in its attempts at orientation.

Butterflies proved to be very convenient to experiment with, since by grasping them by the wings held together above the body they could be held quite steadily, especially with the aid of a hand rest, above the disk. A cabbage butterfly, *Pieris rapæ*, was held facing the center of the disk and presenting its

right side to the light. Almost immediately the butterfly attempted to turn toward the light, and by the action of its legs caused the disk to rotate in the opposite direction. After a few rotations of the wheel the butterfly was turned into the reverse position so that its left side was exposed to the light. Within a few seconds it began to turn the disk away from the light as before. When replaced in its original position the butterfly rotated the disk again toward the left side. Several subsequent trials gave similar results, and another specimen of the same species responded in practically the same way as the one described.

Experiments with *Melitæa chalcedon* gave results very similar to those with the cabbage butterfly. When the insect was held pointing obliquely away from the light it would still turn the disk away from the more illuminated side. When pointing obliquely toward the light the butterfly would give the same response. In every position except that in which the body was parallel to the rays there were efforts to turn toward the light which resulted in the rotation of the disk. If the insect was held facing the light and parallel to and near one edge of the disk, rotary movements were set up as a consequence of attempts at forward locomotion. In many cases the disk would be rotated for several minutes without cessation, and when the butterfly became quiet it could generally be caused to resume its activity by pulling it slightly backwards. In both Pieris and Melitæa the head was kept turned slightly toward the light. *Eurymus eurytheme* and *Cœnonympha californica* also rotated the disk away from the light. Most of the specimens of *Euvanessa antiopa* experimented with failed to give results on account of feigning death so long as they were held, but one individual became active after a time and consistently rotated the disk away from the illuminated side.

Two species of Diptera of the family Tachinidae rotated the disk uniformly away from the light. Other species when held would execute only irregular movements. The same was true of several other phototactic insects belonging to different orders. The aculeate Hymenoptera expended most of their energy in efforts to sting their captor, and attempts to escape in most other cases effectually overcame any phototactic proclivity that may have existed. However, the comparatively few insects

that continued to exhibit light reactions under the unnatural condition of being held between the fingers or by forceps gave such uniform and unequivocal reactions that there can be little doubt that light exercised a continuous stimulating influence upon their activity. The slight movements due to one's hand or the insect's own actions would affect but very little the amount of stimulation received by the eye, and whatever effects would be produced would tend rather to neutralize one another than to give rise to any continuous efforts in one direction.

It is not possible, we believe, to construe phototaxis entirely in terms of differential sensibility. Responses to the shock of transition, whether in the direction of an increase or a decrease of stimulus, may play a part in the orientation of many forms, but the continuous stimulating influence of light appears to be, in several cases at least, the factor of major importance.

A SOLITARY WASP (*APHILANTHOPS FRIGIDUS* F. SMITH) THAT PROVISIONS ITS NEST WITH QUEEN ANTS[1]

WILLIAM MORTON WHEELER

Several years ago a correspondent sent me a few specimens of a beautiful black and yellow wasp, *Aphilanthops frigidus* F. Smith, each mounted on a pin with a winged queen of the typical *Formica fusca* L. These specimens were collected August 21, 1903, at Silver Creek, Baraga County, in northern Michigan, by Mr. Morgan Hebard. Although it seemed very probable that the ants had been taken as the prey of the wasps, I was not sure of this fact till the past summer, when I was able to study the habits of these insects in the neighborhood of Boston. During this season, in fact, they seem to have been so abundant as to have attracted the attention of other entomologists in New England and Canada.

The nearctic genus *Aphilanthops* was first separated from the closely related *Philanthus* by Patton in 1880 and based on *Ph. frigidus* F. Smith as the type. Since that time Cresson (1865), Fox (1894), Baker (1895), Cockerell (1895, 1896) and Dunning (1896, 1898) have described a number of additional species. Eleven of these altogether are enumerated by Dunning in his monograph of the genus (1898), all confined to the western states, except the type *A. frigidus*. This was originally described from Nova Scotia, but is now known to range over Ontario and New England, as far west as Illinois and Chicago and as far south as New Jersey. Two other species from Mexico have been referred to the genus *Aphilanthops* by Cameron, but Cockerell believes that they really belong to the genus *Eucerceris*.

Concerning the habits of *Aphilanthops* nothing has been published, except the following observations by Ainslee (1909) on *A. taurulus* Ckll.: " Early in August, 1908, while marooned at

Albuquerque, New Mexico, waiting for delayed mail, I noticed one day beside a concrete walk that bordered a vacant lot in that city a throng of large red ants which resembled *Pogonomyrmex occidentalis*. The bunch was seething with excitement, and stragglers were continually coming and going. As I watched I noticed a small quadrate-headed wasp drop from the upper air to the hard-trodden soil, alighting without previous reconnoitering. She stood perfectly motionless, not even dressing herself after the manner of her kind when idle. Presently an ant hurried by, busy about nothing, as usual, when instantly the wasp gave chase. The ant dodged and doubled as it fled, but the wasp overtook and seized it after a very brief and intensely active resistance, for a *Pogonomyrmex* is by no means a helpless infant in a skirmish. The wasp and its riotous victim rose heavily into the air and ascended at a sharp angle of flight, until they were lost in the blue of the sky. During the next few minutes I saw the same performance repeated again and again, with variations, until dozens of the ants had disappeared heavenward with the predatory wasps.

"So intent were the wasps on this work that they seemed not in the least disturbed by my presence, and I managed to secure a number of both wasps and ants by taking quick advantage of the struggle always incident to the moment of capture.

"Occasionally an ant, when pursued, would dodge around a blade of grass or rush beneath some welcome shelter and elude its hunter, but this happened in only a few cases. So swift and certain were the motions of the wasps that even with a vantage of six inches or more an ant once followed was almost certainly doomed. The wasps never, so far as I observed, assisted themselves with their wings to gain speed, but played fair with their victims and ran them down. The struggle generally lasted a second or two on the ground, and, as I have said, appeared to be continued fiercely in the air, judging from the frenzied actions of the two as they rose aloft." Ainslee mentions another, possibly undescribed species of *Aphilanthops* which he took at the same time preying on the same ants. Specimens of these, sent me for identification, proved to belong to the large, coarsely sculptured form of agricultural ant, *Pogonomyrmex barbatus* F. Smith subsp. *rugosus* Emery, which makes extensive clearings in the deserts of New Mexico and Arizona. Although not ex-

pressly stated, it is clear from Ainslee's vivid description, that *A. taurulus* preys on the workers of the *Pogonomyrmex*. As will be seen from the following account, our eastern *A. frigidus*, though it also provisions its nests with ants, selects only the fertile females, or queens.

My observations on *frigidus* were made in the Blue Hills, near Boston, during July and August. The wasps were found to be at the height of their activities from July 26 to August 16. By the end of the latter month all the wasps had disappeared and the nests had been effaced by recent heavy showers. Like the species of *Bembex*, *frigidus* nests in colonies. Several of these were located, but observations were confined to three, which happened to be within easy reach from Boston. They were situated in the ravine that separates Great Blue Hill from the adjacent portion of the range, two of them being in the stony and sandy trail passing through Wild Cat Notch, the other on Administration Road. Each colony covered several square yards of territory and comprised from about 30 to 60 nests, the entrances of which were often within an inch or two of one another. In two of the colonies the nests were interspersed with the burrows of large Crabronid wasps and of Cicindelid larvæ. The wasps prefer to make their burrows on slightly sloping surfaces. The opening, a little more than a quarter of an inch in diameter, is semi-circular and lies in front of a little pile of earth that has been thrown out by the burrowing insect. The wasp spends much time, especially during the morning hours or on cloudy days, sitting in her burrow and looking out with her conspicuous black face, marked with three vertical yellow bands like exclamation points. As the heat of the day increases, however, she becomes more active and either does more or less excavating in the nest, kicking the earth out backwards from the entrance to a distance of a few inches, or goes off foraging for her prey. In all of this behavior she exhibits a striking resemblance to *Bembex*.

The burrow descends obliquely and abruptly to a depth of only six to eight inches, where it terminates in a small cell. There are also two or three other cells, but it was found impossible to determine their precise relations to the other portions of the nest, owing to the very dry and crumbling condition of the soil and to the fact that each cell is closed off from the main

burrow. A slender twig or grass culm carefully introduced into the opening of the nest as a probe was invariably stopped a few inches below the surface by an earthen plug or partition which has to be removed by the wasp whenever she enters the deeper portions of the nest.

The prey of *A. frigidus* consists exclusively of winged queen ants belonging to the genus *Formica*. Specimens wrested from the wasps while being brought in and also dug from the nests, belonged to the following four forms:

Formica fusca L. var. *subsericea* Say.

F. fusca L. (typical).

F. (Neoformica) pallidefulva Latr. subsp. *nitidiventris* Emery.

F. (Proformica) neogagates Emery.

Most of the specimens belonged to *subsericea*, very few to *neogagates*, while the true *fusca* was more abundantly represented than *nitidiventris*. The nature of the prey, however, depends on the situation of the *Aphilanthops* colony. Thus the prey in the Administration Road colony, which was situated very near the northern side of Great Blue Hill, consisted almost exclusively of the typical *fusca*, which is the only form of the species on this more boreal slope, whereas the more xerothermic *subsericea* and *nitidiventris* were the only forms found in the colony situated on the southern slope. As these two colonies were less than a mile apart, it is clear that the wasps do not range very far in search of their prey. The same wasp may collect queens of two or even three of the four *Formicæ* enumerated above. The pronounced preference for the queens of *fusca* and its variety *subsericea* is shown also in other portions of the geographical range of *A. frigidus*. I have already stated that the specimens of this wasp taken by Hebard in northern Michigan had been preying on *fusca*. Recently while I was visiting my friend Dr. C. Gordon Hewitt at Ottawa, Ontario, the noted melittologist, Mr. Sladen, showed me a specimen of the wasp taken August 12, 1913, with a winged queen of the typical *fusca*. He pointed out to me the site of the colony where he had seen this and other specimens of the wasps carrying in their prey, in the midst of a cultivated plot on the Central Experimental Farm, but all traces of the nests had disappeared at the time of my visit (September 2). During August, Mr. C. W. Johnson brought me a specimen of *frigidus* mounted on

a pin with a winged female of *subsericea*, which he had taken July 31 at Westport Factory, Mass., where he had found a large colony of the wasps nesting in a pebbly wood-road. They were bringing in the *subsericea* queens in great numbers and, curiously enough, were themselves being captured and destroyed by large robber-flies (*Deromyia umbrina*).

The queens of the four *Formicæ* enumerated above, differ considerably from one another, those of *subsericea* being much larger than any of the others and those of *nitidiventris* differing greatly in color, as they have the head and thorax red instead of black. The queens of the true *fusca* and *neogagates* are much alike in size and in being very smooth and shining, but the latter species is readily distinguished by the red color of the legs and the erect hairs on the lower surface of the head. It is significant that all these queens belong to species noted for their cowardly disposition, and as the normal hosts of the slave-making ants (*Polyergus lucidus* Mayr and the various subspecies of *Formica sanguinea* Latr.) and of a long series of temporary social parasites (the various subspecies of *F. rufa* L., *truncicola* Nyl., *exsectoides* Forel, etc.). Although nearly all of these pre-datory and parasitic ants are abundant in the Blue Hills, none of their queens is captured by the *Aphilanthops*. We must assume, therefore, that this wasp has learned to discriminate between different species of *Formica* and to avoid the more vigorous and aggressive queens of the *sanguinea*, *rufa* and *exsecta* groups. The queens of the *microgyna* group, represented in the Blue Hills by *F. difficilis* Emery, are in all probability avoided on account of their diminutive stature.

That the wasps capture the *Formica* queens while they are celebrating their nuptial flight and do not take them from their nests, was clear from observations made July 26, for on that day flights of *subsericea* and *sanguinea* subsp. *rubicunda* Emery were observed in the Blue Hills and the wasps were seen bringing in numbers of the queens of the former variety. Still I did not see the wasps in the act of capturing their prey till August 15, when there was a great flight from all the colonies of *subsericea* in Forest Hills and Jamaica Plain, Boston. While walking along the street I saw an *Aphilanthops* suddenly swoop down onto a queen that had just settled on the ground. Before I could reach the spot the ant had been stung and the wasp

was dragging her along by the antennæ and trying to rise with her into the air.

The queen ants attract the attention of the wasps only during the few hours that intervene between the nuptial flight and the loss of their wings. On several occasions I saw deälated queens crossing the roads near the wasp colonies or even running near their nest entrances without being noticed by the wasps that were flying about. And on one occasion when I confined a deälated *subsericea* queen in a bottle with an *Aphilanthops*, the ant was still uninjured more than 24 hours later. It is probable, therefore, that the wasp responds only to the visual stimulus of the winged queen, which is, of course, very different from that of the same insect with her wings removed.

The ants are merely stung and paralyzed. The wasp does not mutilate or malaxate her victims, which still move their palpi, legs and antennæ either spontaneously or when touched, for several hours or even for a few days after they have been captured and placed in the nest. In the course of a few days and often sooner, however, all signs of movement have ceased, although the insects still have a fresh appearance, with flexible limbs and without any indications of the drying up of the tissues.

The wasp carries the ant under her body, supporting it by means of her middle and hind legs, while she holds its antennæ in her mandibles. Sometimes when she happens to settle for a moment on a slanting leaf-blade and is therefore obliged to stand on her legs, one may see the ant dangle for a moment from her jaws. On reaching the nest she may begin to enlarge the entrance by digging, still holding the ant by its antennæ and kicking the earth backward around it with her hind legs. Sometimes she may go directly into the nest without any preliminary digging and without dropping her prey. Occasionally, however, she may be seen to drop it just at the entrance, then go into the burrow, turn around and pull the ant in after her by one of its antennæ. This method of getting the ant into the nest is sometimes very awkwardly executed. Once I saw a wasp seize her ant by the petiole and with much effort pull it in doubled on itself. While the wasp is taking the ant into the burrow, she may be closely watched by two parasites, a beautiful metallic green *Chrysis*, or cuckoo-wasp, and a small gray Tachinid fly. I have not seen either of these insects oviposit

on the wasp's prey, nor have I found their larvæ in the nests. The wasp usually introduces her prey into the burrow so expeditiously and then buries it so completely that these parasites must encounter great difficulties in gaining access to it.

After the ant has been dragged a few inches down the burrow, the wasp proceeds to cut off its wings. Usually she does this very neatly, although the stubs she leaves attached to the body are a little longer than they are in queen ants that have dealated themselves. More rarely the wasp simply gnaws off the tips or apical halves of the wings. That this dealation is accomplished before the ant is carried to the lower portion of the nest is shown by the fact that while excavating the nest one always finds the detached wings only a few inches below the surface and some distance from the bodies of the stored ants.

Although I excavated a considerable number of nests with the aid of Messrs. W. M. Mann and F. X. Williams, I have had some difficulty is ascertaining the precise method employed by the *Aphilanthops* in rearing its young. By piecing together the observations made on different nests I have reached the conviction that the wasp secures several queen ants, usually five to seven, often belonging to more than one species, and stores them in two or three cells. Sometimes only a single ant is deposited in a cell, more frequently two, rarely three. No eggs were to be found on such stored individuals, but in each of two nests, a young larva was found in a small cell devouring a single ant, which had been cut in two at the petiole. The mother *Aphilanthops* was sitting in the burrow in each of these nests and in one of them there was a paralyzed ant in a chamber separated from the one in which the larva was feeding. Several older nests were excavated in which there was a single adult larva spinning its cocoon and surrounded by fragments of three or four queen ants. These conditions seem to me to prove that the *Aphilanthops* feeds her single larva from a store of several ants deposited in several cells. The egg is evidently laid on an isolated ant which the mother wasp cuts in two in order that the larva may gain access to the nutritious contents of the thorax and gaster. Then the other ants are taken from storage and brought to the larva one by one as they are required, till all are consumed and the larva is ready to pupate. As the wasps were found in the nests even after the larvæ had pupated and

in nests containing old and empty cocoons and freshly stored ants but no larvæ, we may infer that after one larva has been reared in the manner described above the mother sets about providing for another in the same nest but in a fresh chamber. Pupæ nearly ready to hatch were found August 5 and freshly pupated young August 16; young larvæ were found on the latter date and on August 8. The larva and cocoon closely resemble those of *Cerceris rybiensis* as figured by Marchal (1887).

If my interpretation of the feeding of the larva is correct, we have in *Aphilanthops* a very interesting condition intermediate between that of the great majority of solitary wasps, which first collect provisions and then lay an egg upon them, and that of *Bembex*, which lays its egg on a single fly and feeds the hatching larva from day to day with fresh flies. If Fabre is right in supposing that *Bembex* does not always give all the captured prey to its young but keeps a portion of it temporarily out of the larva's reach in the burrow, we should have an approach to *Aphilanthops*, which brings in its store before beginning to feed its larva. This temporary storing of ants and the fact that they are not killed outright as in *Bembex*, but merely paralyzed, calls for an explanation. This, I believe, must be sought in the peculiarity of the prey, which is quite unlike that of other solitary wasps in that it can be obtained only at considerable and irregular intervals of time, namely, during the marriage flights of the various species of *Formica*. These flights may, to be sure, occur any time between the middle of July and the first of September, but nearly all the colonies in a given locality celebrate their flight on the same date and often during only a few hours, so that many days may elapse before there is another flight. And although the wasps draw their supply of prey from several different species of *Formica*, this does not very greatly improve matters. In any event, the wasps have to make hay while the sun shines and carry in as many ants as they can secure before beginning to rear the larvæ. The need of thus temporarily storing the prey also explains why it is paralyzed and not killed outright as in the case of *Bembex*, nor mutilated before it is really fed to the young. Of course, it is not impossible that the Bembecine method may also be employed by *Aphilanthops* if nuptial flights of the ants occur in quick succession so that there is no need to store the prey before

feeding it to the young, but whether this is the case or not can be determined only by future observations.

The behavior of *Aphilanthops* stands out in an interesting light by comparison with that of the other genera of Philanthidæ, *Philanthus* and *Cerceris*, which, unlike *Aphilanthops* are represented by several species in Europe as well as in North America. Fabre (1891) has given us a fascinating account of *Philanthus apivorus* (=*triangulum*), which preys on the honey bee. He shows how this wasp kills the bee outright and then gorges itself with the honey which it presses out of the body of its victim. This extraordinary behavior he explains as a necessary adaptation to the diet of the larva, as he found by experiment that the insect in this stage thrives on nitrogenous food but is poisoned if it eats honey. The great depth of the nest of *Ph. apivorus* is given as one meter. The egg is laid on a dead bee and recently killed bees are fed to the growing larva from time to time after the manner of *Bembex*. Fabre also made some observations on *Ph. coronatus* Fabr. and *venustus* Rossi (=*raptor* Lep.) and found that the former provisions its nest with larger, the latter with smaller bees of the genus *Halictus*. He believes that in these cases also the honey is expressed from the bodies of the victims, but this opinion has not been confirmed. Ferton (1905) has also studied *Ph. venustus* and enumerates 14 different species of *Halictus* and one of *Andrena* which he found in the nests. He calls attention to the depth of the burrows but says nothing about the method of feeding the larvæ;

The only American *Philanthus* whose habits have been described is *Ph. punctatus* Say. According to the Peckhams (1898) this wasp nests in very small colonies and preys on bees of the genus *Halictus*, which it kills outright, but it does not malaxate them, nor express the honey from their bodies. The main burrow of the nest reaches a length of 22 inches. The following quotation shows that the method of rearing the young is very different from that described by Fabre for *Ph. apivorus:* " We did not find distinct pockets, as the soil was very crumbly and fell in as we worked, but we came upon clumps of bees an inch or so to one side of the gallery and about three inches apart, with larvæ in different stages of development. In one nest we found 26 bees in two clumps, some of them half-eaten

and some of them fresh, but all quite dead. We have no doubt that punctatus completely provisions one pocket and closes the opening from it into the gallery, before she starts another, making a series of six or eight independent cells. The provision for one larva is probably 12 or 14 bees, the capture of which, in good weather, would be a fair day's work." Melander and Brues (1903) have seen this same species of *Philanthus* nesting in the midst of colonies of *Halictus pruinosus* Roberts. and ruthlessly preying on the bees.

We are also in possession of a number of published observations on various species of *Cerceris*. Fabre (1894) describes the habits of several of these. One of them (*C. bupresticida* Duf.) provisions its nest with Buprestid beetles, five others (*C. arenaria, ferreri, truncatella* (=4-*cincta*), *labiata* and *julii*) prey on weevils and another (*C. rybiensis* =*ornata*) preys on bees of the genera *Halictus* and *Andrena*. Marchal (1887) shows, in a beautiful study of this last species, that the wasp not only stings the bee but also crushes, or malaxates the back of its neck and laps up the exuding juices and honey. As a result of this treatment the bee dies in the course of a few hours. Adlerz (1900, 1903) lists *C.* 5-*fasciata, arenaria* and *truncatella* as provisioning their nests with weevils, *C. hortivaga* as preying on bees of the genus *Hylæus* and *C. labiata* as collecting both Chrysomelid and Curculionid beetles. Ferton (1901, 1905) cites *C. specularis, truncatella* and *ferreri* as preying on weevils, *C. emarginata* on bees of the genera *Halictus, Prosopis* and *Andrena*, and *C. magnifica* on *Halictus* and *Andrena*. This last species laps the honey from the body of its victim through a hole made in the back of its neck, as described by Marchal in the case of *C. rybiensis.*

The Peckhams (1898, 1900) find that the American *C. clypeata* Dahlb., *deserta* Say and *nigrescens* F. Smith all prey on weevils, like the majority of European *Cerceris*, but that *C. fumipennis* Say preys on a Buprestid beetle, *Chrysobothris* 4-*impressa*, which it kills outright. In all the species of *Cerceris* observed up to the present time the cell is first provisioned with numerous specimens of the prey, the egg is then laid and the cell closed as in the great majority of solitary wasps.

It would seem, therefore, that the method of rearing the young in *Aphilanthops* is intermediate between that of *Cerceris* and *Philanthus punctatus* on the one hand and of *Ph. apivorus*

on the other. The question then presents itself: Do *Ph. apivorus* and *A. frigidus* represent an advance on *Cerceris* or are the conditions in this genus derived from those of *Ph. apivorus?* In other words, is the Bembecine a primitive or a secondary method of caring for the young among the solitary wasps? Undoubtedly most observers would be inclined to regard *Bembex* as representing a later phylogenetic stage and one leading to the conditions in the social wasps, but the Peckhams take a different view. "It may be possible, then," they say, "that all wasps originally fed their larvæ from day to day as *Bembex* now does, and that while the instinct of paralyzing the prey and of storing the whole supply of food once for all was working itself out among the solitary wasps, the instincts connected with life in a true society, and of joining together in the work of feeding the larvæ, have, on the other hand, developed into those of our wasp communities."

It is difficult to decide between the evolutionary alternatives here indicated, but analogy with the phylogenetic history of the bees, in which two precisely similar methods of rearing the young occur, certainly points to the Bembecine method as secondary. This view is also sustained by the sporadic and independent occurrence in several highly specialized groups of wasps of this method as the one best adapted to certain peculiar conditions. Such cases are *Aphilanthops frigidus* and *Philantus apivorus*. Two others are cited by the Peckhams, one in the genus *Sphex* (*Ammophila*), where they found "an instance which looks like a connecting link between the habits of *Bembex* and those of the solitary species. *A. urnaria* stores one caterpillar, lays an egg on it, catches another and stores it as soon as she can and then closes the nest. As a usual thing, no doubt, the nest is finally closed before the egg is hatched, so that she never sees her larva. In one of our instances, however, the capture of the second caterpillar was so much delayed that when it was brought in the mother wasp found a larva of a day old feasting on the one already provided." The other case is that of *Lyroda subita* Say, which these authors found to resemble *Bembex* in feeding its larva from day to day on small crickets. Most instructive in this connection, however, is the *Aphilanthops*, because its method of collecting a supply of queen ants before feeding them one by one to the growing larva, indi-

cates very clearly that this wasp originally had the storing habits of the allied genus *Cerceris* and of *Philanthus punctatus* and has secondarily acquired the Bembecine method of feeding its young. I am, therefore, inclined to regard the Bembecine method as derivative, or secondary, and find further confirmation of this view in the fact that in all cases, except *Lyroda*, the prey of those solitary wasps which feed their larvæ from day to day, belongs to highly specialized groups of insects of comparatively recent phylogenetic origin—ants in the case of *Aphilanthops*, honey bees in the case of *Philanthus apivorus* and higher Diptera in the case of *Bembex*.

The species of *Aphilanthops* are not the only solitary wasps that prey on ants, for some four small Mediterranean Crabronids, belonging to two genera, are known to provision their nests with these insects. Ferton (1890) describes the habits of *Fertonius luteicollis* Lep. in Algiers, where it digs its nest in sandy soil, making burrows only about 4 cm. deep, but also nests in the crevices of walls. It preys exclusively on workers of *Tapinoma erraticum* Latr., storing in each cell 40 to 50 of these strong-smelling ants, which are merely paralyzed and far from motionless at first. There are three generations of the wasps in the course of the year. Later (1895) Ferton described from Corsica a second species of the same genus (*F. formicarius* Fert.) which also preys on *Tapinoma erraticum* workers and closely resembles *F. luteicollis* in its other habits. In 1893 Emery described the habits of *Brachymerus curvitarsis* H. Sch., a Crabronid that preys on the workers of *Liometopum microcephalum* Panz. in Italy. He saw it pounce on the ants as they were moving along in files. The nest was found in a fig-tree, in the abandoned burrows of a longicorn beetle. The ants were stored in numbers (about 40) in each cell and were "imparfaitement paralysés, quelques uns capables même de se trainer sur leur pattes." More recently (1901) Ferton has figured a second species of the same genus (*B. 5-notatus* Jur.) which, like the species of *Fertonius*, preys on workers of *Tapinoma erraticum*.

It is interesting to note that all of these Crabronids prey on strong-smelling ants of the subfamily Dolichoderinæ and that they select only the workers. Ainslee's observations show that the latter statement is also true of *Aphilanthops taurulus* but

that in this case Myrmicine ants are selected. *A. frigidus,* as I have shown, confines its depredations to Camponotine ants of the genus *Formica* and selects only the queens, which are, of course, the largest and most nutritious caste. This specialization in diet, while highly advantageous to the wasps, is very destructive to the ants, since each fecundated queen is really a potential colony. Still the prey preferred by *frigidus,* namely *F. fusca* and its var. *subsericea,* notwithstanding the depredations of the wasps and of our numerous slave-making and temporarily parasitic species of *Formica,* maintain their status as far and away the most abundant ants of their genus in the northeastern states and Canada. They are able to support this greedy host of prædators and parasites because they are extremely prolific, hardy, or eurythermic, and of a very industrious and peaceable disposition.

LITERATURE.

ADLERZ, G.   Biologiska Meddelanden om Rofsteklar.   *Ent. Tidskr.*, 1900, pp.
  1900.   161–200.
  1903.   Lefnadsförhållanden och Instinkter inom Familjerna Pompilidæ och
      Sphegidæ. *Kgl. Svensk. Vetenskaps. Akad. Handl.*, XXXVIII,
      No. 5, 1903, pp. 1–181.
AINSLEE, C. N.   A Note on the Habits of Aphilanthops.   *Canad. Ent.*, XLI, 1909,
  1909.   pp. 99–100.
BAKER, C. F.   Notes on Aphilanthops.   *Canad. Ent.*, XXVII, 1895, pp. 335–
  1895.   336.
COCKERELL, T. D. A.   Descriptions of New Hymenoptera.   *Trans. Amer. Ent.*
  1895.   *Soc.*, XXII, 1895, pp. 289–297.
  1896.   Still Another Aphilanthops.   *Canad. Ent.*, XXVIII, 1896, pp. 221–222.
CRESSON, E. T.   Monograph of the Philanthidæ of North America.   *Proc. Ent.*
  1865.   *Soc. Phila.*, V, 1865, pp. 85–132, 4 figs.
DUNNING, S. N.   Notes on Aphilanthops and Description of a New Species.   *Canad.*
  1896.   *Ent.*, XXVIII, 1896, pp. 203–206.
  1898.   Monograph of the Species of Aphilanthops Inhabiting Boreal Amer-
      ica. *Trans. Amer. Ent. Soc.*, XXV, 1898, pp. 19–26.
EMERY, C.   Sur un Crabronide Chasseur de Fourmis.   *Bull. Soc. Ent. France,*
  1893.   1893, pp. LXIII–LXIV.
FABRE, J. H.   Souvenirs Entomologiques.   4e *Sér.*, 1891, pp. 191–218.
  1891.
  1894.   Souvenirs Entomologiques.   1c *Sér.*, 3e Ed., 1894, pp. 39–66.
FERTON, C.   Un Hyménoptère ravisseur de Fourmis.   *Act. Soc. Linn. Bordeaux,*
  1890.   5e *Sér.*, 1V, 1890, pp. 341–346.
  1895.   Nouveaux Hyménoptères Fouisseurs et Observations sur l'Instinct de
      quelques Espèces. *Act. Soc. Linn. Bordeaux,* 5e *Sér.*, VIII, 1895,
      pp. 261–272.
  1901.   Notes Detachés sur l'Instinct des Hyménoptères mellifères et ravis-
      seurs avec la description de quelques espèces. *Ann. Soc. Ent. France,*
      LXX, 1901, pp. 83–148, 2 pls.
  1905.   Notes Detachés, etc.   3e *Sér.*, *Ann. Soc. Ent. France,* LXXIV, 1905,
      pp. 56–104, 2 pls.
MARCHAL, PAUL.   Etudes sur l'Instinct du Cerceris ornata.   *Arch. Zool. Expér.*
  1887.   *Gén.*, 2e *Sér.*, V, 1887, pp. 27–60, 6 figs.
MELANDER, A. L. and BRUES, C. T.   Guests and Parasites of the Burrowing Bee,
  1903.   Halictus.   *Biol. Bull.*, V, 1903, pp. 1–27, 7 figs.
PATTON, W. H.   Notes on the Philanthinæ.   *Proc. Bost. Soc. Nat. Hist.*, XX,
  1880.   1880, pp. 397–405.
PECKHAM, G. W. and ELIZABETH G.   On the Instincts and Habits of the Solitary
  1898.   Wasps. *Wis. Geol. and Nat. Hist. Survey*, Bull No. 2., 1898, 245
      pp., 14 pls.
  1900.   Additional Observations on the Instincts and Habits of the Solitary
      Wasps. *Bull. Wis. Nat. Hist. Soc.* I, 1900, pp. 85–93.
SMITH, F.   British Museum Catalogue.   Hymenoptera, IV, 1856, p. 475.
  1856.

NOTES

SINGING MICE

C. A. COBURN

The Harvard Psychological Laboratory

Volume 2, number 5, of this journal contained a report of observations made on a "singing" mouse. This individual, a female, was bred with both wild and tame males but the singing did not appear in any of her thirty-three offspring.

In November, 1912, a singing mouse, a female, was discovered in the home of an Italian family in New York City. It was reported to the Harvard Psychological Laboratory and later brought here for observation.

With it was captured a full-grown male and two young, probably her mate and young. She was bred with this male but, as in the former case, no "singers" appeared.

In March, 1913, a farmer in Michigan caught a "singing" mouse which he thought was a male. It was sent here for breeding purposes, but it, too, proved to be a female.

It has been claimed that the singing occurs only in females. The writer is very anxious to learn whether this is true. He will be grateful for any information which other observers may be able to send him. He is especially desirous of obtaining "singing mice" in order to determine whether the behavior is inheritable.

Persons who have either direct or indirect knowledge of "singing" individuals are requested to communicate with the writer at the Harvard Psychological Laboratory, Emerson Hall, Cambridge, Mass.

LITERATURE FOR 1912 ON THE BEHAVIOR OF LOWER INVERTEBRATES

S. J. HOLMES
The University of California

The experiments of Allee (1) were performed mainly upon *Asellus communis*. Specimens from streams gave a high percentage of positive rheotactic responses. Pond isopods, on the other hand, showed a weak positive rheotaxis, and were frequently indifferent. In general the oxygen content of streams was found to be higher than in ponds. That this fact may afford at least a partial explanation of the different responses of pond isopods and stream isopods is indicated by results of experiments which showed that the positiveness of the rheotaxis is decreased by lack of oxygen. In general agents that act as depressants (chloretone, potassium cyanide, carbon dioxide, low temperature, etc.) reduce the rheotactic response, while agencies that stimulate metabolism, such as oxygen, caffein and increase of temperature within certain limits, increase this response.

Bauer (2) has shown that the behavior of *Pecten jacobaeus* L. is unusually complex and shows many interesting adaptations to its habitual environment. This species feeds mainly on microscopic algae, and seeks well lighted situations which naturally afford more of its accustomed food. During the process of swimming, which is accomplished by opening and closing the valves of the shell, the animal is unable to orient itself to the rays of light. Orientation is effected when the Pecten comes to rest on the bottom, by forcibly expelling the water on the side that is turned away from the light. After being turned so as

to face the light, the animal begins to swim through the water for a short distance, then settles down, reorients itself and makes another excursion. Pecten frequently closes its shell upon the approach of a large moving object, and the experiments of the author have convinced him that this reaction is not a shadow reflex such as is performed by many other mollusks, but a reaction based upon the movement of the object in its field of vision.

The numerous tentacles that fringe the margin of the mantle are organs that are very sensitive to touch and chemical stimulation. If the tentacles come in contact with a starfish the mollusk commonly swims away. The juices of the starfish diffusing in the water evoke the same lively response. If Pecten, which commonly lies upon its more convex right side, is turned over it is able to right itself by opening and closing the valves of the shell. Bauer concludes from several experiments that both the eyes and the statocyst are concerned in the righting reaction.

Bohn (3) has discovered that in actinians pressure of the water in which they are contained tends to cause them to expand. Certain copepods and the larvae of the lobster may be caused to react negatively to light by only a slight increase of the pressure of the water.

Bohn (4) believes that there are two kinds of sensitivity, one to light, another to shade, corresponding to antagonistic chemical reactions. Causes that accelerate oxidations tend to make animals positively phototactic; causes that inhibit oxidations produce attraction to shade. Periods of sensitivity to light tend to alternate with periods of sensitivity to shade. Young lobsters are rendered temporarily positive to light by acids and more permanently positive by alkalis.

Planarians which had been illuminated on one side and which had been turning away from the source of stimulus were found by Boring (5) to keep turning toward the opposite side after being transferred to a situation in which the light was the same on both sides of the body. Apparently the more stimulated side had lost some of its sensitivity. After turning away from the light for a while the planarian begins to make sudden turns toward the light which for a time increase in frequency, but finally disappear. Boring considers these turns to be "a form

of compensatory muscular movement, initiated as a relief from the continued contraction of the muscles already involved in turning."

Chidester (6) gives a general account of previous work on the biology of the crayfish (with bibliography), and original observations on feeding, reactions to light, and behavior of young. Crayfish are positively phototactic in weak and negative in strong light. They are most active at night.

Clementi (7) has studied the effect of cutting the nervous cord and of removing parts of the central nervous system upon the movements of Julus. Merely cutting the ventral nerve cord does not destroy coördinated movements of locomotion; the wave-like movements of coördinated action of the legs pass over the region of the severed cord much as they do in a normal animal. Removal of the three anterior segmental ganglia of the ventral cord profoundly affects the coördination of the loco-motor appendages, and destroys the possibility of performing certain reactions.

In the course of his extensive monograph on the Acinetas, Collin (8) gives a general account of the behavior of these organisms and discusses the mechanism of their movements.

Embody (9) has studied the distribution, food habits, mating behavior and general activities of several fresh water amphipods.

Ewald (10) finds that the larvae of *Balanus perforatus* are affected by sudden changes in the intensity of light. "Increase of illumination causes inhibition of locomotion, preceded by a slight acceleration; the result is a sinking. Decrease of illumination causes acceleration of locomotion." Green and yellow-green light are the most potent in evoking these reactions as well as in effecting orientations.

Increase of temperature tends to produce a negative reaction while decrease of temperature has the reverse effect. A sodium chloride solution isotonic with sea water makes negative animals positive. Potassium chloride has a similar but weaker effect, while an isotonic calcium chloride solution causes the larvae to swim about without regard to the light. Magnesium acts as an antagonist to sodium. If $MgCl_2$ is added to a pure $NaCl$ solution it tends to evoke a negative reaction. The hydrates of ammonia and sodium produce a negative reaction, while HCl, H_2SO_4 and HNO_3 have the reverse effect; acetic acid and CO_2

have little influence on the reaction. Increase of concentration by the addition of NaCl or Mg Cl$_2$ had a strong positivating effect, while hypotonic solutions of these salts produced the opposite result. The action of various stains was tested, but the effects produced were small and of uncertain interpretation.

Dr. Franz (11) is of the opinion that the rôle of phototaxis in determining the vertical migration of marine animals is not only unproven but improbable. That fewer animals are caught in a net near the surface during the daytime is attributed to the fact that the animals can see the net better at that time and so escape from being caught. At night they are unable to avoid the net and are hence caught in greater numbers near the surface.

This conclusion is in part based on the author's conviction that phototaxis is frequently a product of artificial conditions of confinement in a laboratory. Many organisms, according to Franz, react to light in aquaria which do not show any phototaxis in their natural habitat. Phototaxis is based on movements of escape (Fluchtbewegung), and when it is manifested by animals in nature it is an expression of an effort to get into a free environment or to seek the protection of a secluded nook.

According to Hadley (12) only well fed lobsters of the fourth larval stage will respond to light. Hungry individuals do not burrow so readily as those which are well fed, but they are much more active in swimming. Clam juice in the water tends strongly to make the young lobsters swim at the surface, especially if they have been kept without food.

According to Hargitt (13) there is little relation between the position of the tubes of a number of sedentary annelids (*Protula protula*, *Hydroides pectinata*, *Potamoceras triqueter* and *Spirographis spallanzanii*) and the direction of the light that habitually falls upon them. In general, Hargitt's experiments confirm his previous results on these and other tubicolous annelids. There is a discussion of the relation of the results secured to the theory of tropisms and the general explanation of animal behavior.

Harper (14) has carried on experiments to ascertain how the geotropism of Paramecium is affected by feeding the animals with finely divided iron. As the particles accumulate in the posterior end of the body this part tends to sink downward, and

this causes the animal to swim upward unless the load is too heavy. As the particles of iron become more evenly distributed through the body the negative geotropism tends to disappear. A strong magnet placed at one side of a dish containing Paramecia which have ingested iron causes the animals to swim upwards until they reach a weaker part of the magnetic field.

Henri and Henri (15) and Henri and Larguier des Bancels (16) (17) in several papers have given an account of their experiments upon the reactions of Cyclops to ultra-violet rays. These rays stimulate the animals to rapid activity, but if the duration of the stimulus is too short no reaction is produced. When the stimulus is of longer duration the Cyclops respond uniformly after a certain interval of time, which remains remarkably constant for many successive experiments. The latent period is decreased as the intensity of the stimulus is increased. Starting with a stimulus which does not last long enough to evoke a reaction, it is found that if a number of stimuli are applied in rapid succession, the effect is the same as if the stimulus were applied continuously throughout a period equal in length to the sum of the partial stimulations. If the stimuli are separated by longer intervals, there is a partial summation of the effects, which diminishes with the increase of the interval until it is no longer apparent. The authors discuss the relationship of these results to certain phenomena of memory in man.

The sea-urchin *Arbacia punctulata* was found by Holmes (18) to react negatively to light of a great range of intensity, although it is occasionally positive in weak light. After it has ceased to respond it may be made to resume its phototactic movements by mechanical disturbance. Movements are effected by the combined action of the spines and tube feet, although the animal may crawl away from the light when either of these sets of organs has been removed. Arbacia responds to shadows by erecting the spines, while local stimulation by light causes the spines to bend towards the stimulated region. Strong light thrown upon the tube feet causes them to be withdrawn. Phototaxis is not dependent upon stimulation of both sides of the body. A sea-urchin which is stimulated only by a small spot of light will crawl away from the course of stimulus in a fairly direct line. Cutting the oral nerve ring, while not interfering with the

reactions of particular organs to light, destroys the phototaxis of the organism.

Issel (19) has studied the habits of a small isopod, Zenobiana, which lives in holes in marine plants which it is thought to excavate. The isopods are more active during the night. Shadows cause them to retreat quickly into their tubes. They are strongly thigmotactic and exhibit the instinct of feigning death. There are a number of interesting structural adaptations and instincts in relation to a tube-dwelling life.

Jackson (20) writes a general account of the natural history of *Hyalella knickerbockeri* (Bate), treating of general distribution and local habitat, color changes, size in relation to sex, methods and frequency of molting, breeding habits, food and feeding, enemies, thigmotaxis and locomotion.

Jacobs (21) finds the resistance of different species of Protozoa to CO_2 variable. The contractile elements in Vorticella and Peranema are soon paralyzed, but the cilia and flagella are more resistant. In Vorticella, however, the contractile elements are first stimulated and then paralyzed; the vibratile ones are temporarily stopped and then started again.

It is well known that leaves are commonly drawn either by the tip or petiole into the burrows of earthworms. According to J. Jordan (22) the worms do not examine various parts of the leaf as they were believed to do by previous observers, but they catch hold of the leaf at any point and attempt to draw it in. When leaves are seized by the side this attempt is usually fruitless, and only in those cases in which the worm comes to seize the leaf at some narrow part are the efforts of the creature successful. In most of the previous experiments on this subject the actual behavior of the worms was not witnessed, but Jordan has based his conclusions upon observation of the activities of the animals in weak light.

H. Jordan (23) finds that neither the marginal sense organs nor the margin of the umbrella of the jelly-fish Rhizostoma are necessary for the production of rhythmical contractions. Cyanea becomes more irritable to external stimuli after the margin of the umbrella is removed; removal of the sense organs affects the irritability of the animal but slightly. The author considers that the nervous centers of the margin have the function of regulating the reflex irritability of the animal.

Kew (24) finds that the pairing behavior of pseudoscorpions is in many respects similar to that of scorpions. Fertilization in Chelifer and Chermes is effected by means of a spermatophore.

The first part of Laubmann's (25) paper on the cutaneous sense organs of the Caridea is concerned with the structure and innervation of the sensory hairs on various parts of the body. The physiological experiments of the author showed that the chief organ of smell was the so-called olfactory branch of the first antennae, and that the second antennae and the mouth parts had an olfactory function also.

The locomotion of Peranema when swimming freely was found by Mast (26) to be quite similar to that of Euglena, but ordinarily when not strongly stimulated the flagellate crawls forward along the surface of some solid by wave-like contractions of its body combined with a rotary movement of the tip of the flagellum. When the flagellum encounters an object "the animal bends always toward the larger lip, then proceeds on a new course more or less at right angles with the old. The same response can be induced by contact stimulation of any part of the body or by chemical stimulation." Peranema frees itself from a confined situation by increasing the vigor of beat of the flagellum and by turning the body toward the larger lip.

Matisse (27) has discovered that in the earthworm *Allolobophora putris* the rapidity of locomotion not only varies with the temperature, but at any given temperature it is subject to somewhat complex rhythmical fluctuations. Within certain limits increase of temperature is accompanied by an increase of locomotor activity, which is attributed to the increased rapidity of chemical changes in the tissues. When kept at a constant temperature the worms showed, in addition to a constant decrease of activity, a diurnal rhythm, being more active in the morning and less active later in the day. And superimposed upon this are shorter rhythms of greater and less rapidity of locomotion while the worms are crawling about. The author attempts to correlate these facts with certain peculiarities of the action of catalytic and autocatalytic substances.

In a paper on the general life history of two ciliate infusorians Moody (28) has made some observations upon the behavior of these forms in relation to food. Both forms live upon a particular kind of prey and fail to react to other organisms.

Actinobolus attacks the infusorian Halteria while Spathidium captures *Colpidium colpoda*. If Spathidium is well fed it makes no efforts to capture food.

Moore (29) finds that negative phototropism in *Daphnia pulex* is caused by ultra-violet light below a certain wave length, and that the reaction may be reversed by the addition of small amounts of CO_2 and HCl.

Strychnine added to water containing positive and indifferent specimens of Diaptomus caused a negative reaction in one minute. Atropine produced the same change, but the effect was not so decided, while caffeine produced a positive reaction. Acids and camphor reverse the negative reaction caused by strychnine.

In two papers Orton (31) (32) describes the natural history and general feeding habits of *Crepidula fornicata*, with comparisons between the food habits of this species and those of other mollusks. Several years ago *Crepidula fornicata* was introduced upon the coast of England, where it is proving an enemy of the oyster since it lives upon the same kind of food and thrives in the same kinds of localities. The radula of Crepidula is not used directly in feeding as it is in most gastropods, but is used as a grasping organ for seizing the food. The food material, which consists of minute organisms in the water, is brought in much as in lamellibranchs by the action of cilia on the gills and mantle chamber which sweep currents of food toward the mouth.

Anemones will respond to a stimulus applied to the ectoderm of the base of the column by a contraction of the entodermic muscles of the mesenteries. By a method of staining with silver nitrate a nervous network may be demonstrated in the lamella of the column, and through this network a connection is established between the ectoderm and the mesenteric muscles. Certain responses in animals whose ectoderm has been anesthetized with magnesium sulphate are regarded by Parker as a non-nervous direct response of the muscles.

Pearse (34) has written an account of the general behavior of fiddler crabs, treating of burrowing, feeding, pugnacity, fear reactions and courtship. Like other crustaceans fiddlers show no social instincts, although they commonly live in close association. The males are pugnacious, attacking one another by means of their large chelae. Occasionally males attack females,

and sometimes the females wage ineffectual conflicts with one another. Although the males may perform various antics before the females during the breeding season, Pearse found no convincing evidence of the occurrence of sexual selection.

Polimanti (35) finds that many crabs feign death in various positions and assume various attitudes. The species that are habitually exposed show the response in a more pronounced form than species that bury in the sand or live symbiotically with sponges. The duration of the feint depends upon a variety of external stimuli, but is little influenced by the substratum, light, or visual stimulation of passing objects. The death feint is not a voluntary reaction nor a manifestation of hypnosis, but a special "tonic reflex."

Rynberk (36) in a general review of the subject of the segmental functions of the nervous system gives an account of the analysis of many of the instincts of the lower invertebrates.

In *Stenophora juli* Sokolow (37) finds that progressive movements are caused not by a contraction of myonemes, but through the secretion of gelatinous threads at the posterior end of the body. In acid media which dissolve these threads there is no progressive locomotion, although other movements of the body occur for which the myonemes are responsible. The rate of movement increases with temperature up to an optimum of 28° to 29° C., with maximum at 49° to 42° C., minimum at 4° to 5° C.

Vieweger (38) has made a detailed study of chemotaxis in Paramecium and Colpidium, treating especially of the influence of various combinations of chemicals upon the different tropisms of the animals.

Weymouth and Richardson (39) find that the food of *Emerita analoga*, the common sand mole of the sandy beaches of western North America, consists of microscopic organisms, strained from the water by means of the highly modified antennae which are furnished with numerous fine hairs. As the waves retire from the beach the Emeritas thrust out their antennae from the sand, and then draw them back again when the water has drained off; then they fold in the antennae, which deliver the food to the mouth parts, which are highly modified to deal with the catch of microscopic forms. The sand moles are well adapted by the form of the body and the character of the appendages for

burrowing in the sand, and there are specialized structures adapted to respiration in the peculiar habitat of these animals.

The earthworms tested by Yerkes (40) were induced to crawl through a passage which led to a second one running at right angles to it, so that the animals had a choice of crawling either to the right or to the left. One of these passages was furnished with sand paper and electric wires, so that the worms which crawled into this passage would encounter stimuli which would cause them to turn back. Most of the experiments were carried on with a single specimen which was given a certain number of trials a day for some months. The worm after from twenty to one hundred trials came to avoid the branch of the tube where it received a shock, but its subsequent behavior was far from constant. The habits of turning that were formed were found to persist after the removal of the first five segments of the body and hence the brain. As the brain regenerates the worm shows more initiative and variability in its behavior.

Whether the modified behavior of the worm studied rests upon the formation of associations or upon some other physiological factor or factors is a question difficult to determine in a creature like the earthworm, but if associative memory should be proven in this case it would afford the first instance of this faculty among animals so low in the scale of life.

REFERENCES

1. Allee, W. C. An Experimental Analysis of the Relation between Physiological States and Rheotaxis in Isopoda. *Jour. Exper. Zool.*, **13**, 269-344.
2. Bauer, V. Zur Kenntniss der Lebensweise von *Pecten jacobaeus* L. Im besonderen über die Funktion der Augen. *Zool. Jahrb., Abt. f. allg. Zool. u. Physiol.*, **33**, 127-150.
3. Bohn, G. La sensibilité des animaux aux variations de pression. *C. r. Acad. Sci.*, Paris, **154**, 240-243.
4. Bohn, G. Les variations de la sensibilité en relation avec les variations de l'état chimique interne. *C. r. Acad. Sci.*, Paris, **154**, 388-391.
5. Boring, E. G. Note on the Negative Reaction under Light Adaptation in the Planarian. *Jour. Animal Behav.*, **2**, 229-248.
6. Chidester, F. E. The Biology of the Crayfish. *Am. Nat.*, **46**, 279-293.
7. Clementi, A. Sui Mecanismi Nervosi, che regolono la Coordinazione dei Movimenti nei Diplopodi. *Zool. Jahrb., Abt. f. allg. Zool. u. Physiol.*, **31**, 277-296.
8. Collin, B. Étude monographique sur les Acinétiens. II. Morphologie, Physiologie, Systématique. *Arch. Zool. exp. gén.*, **51**, 1-457.
9. Embody, G. C. A Preliminary Study of the Distribution, Food and Reproductive Capacity of some Fresh Water Amphipods. *Int. Rev. Hydrobiol. u. Hydrogr.*, Biol. Suppl., III Série, Heft 2, 1-38.
10. Ewald, W. F. On artificial modification of light reactions and the influence of electrolytes on phototaxis. *Jour. Exper. Zool.*, **13**, 591-611.

11. Franz, V. Zur Frage der vertikalen Wanderungen der Planktontiere. *Arch. f. Hydrobiol. u. Planktonkunde,* **7,** 493-499.

12. Hadley, P. B. Reactions of Young Lobsters Determined by Food Stimuli. *Science,* N. S., **35,** 1000-1002.

13. Hargitt, C. W. Observations on the Behavior of Tubicolous Annelids, III. *Biol. Bull.,* **22,** 67-94.

14. Harper, E. H. Magnetic Control of Geotropism in Paramœcium. *Jour. Animal Behav.,* **2,** 181-189.

15. Henri, Mme. V. and Henri, V. Excitation des organismes par les rayons ultra-violets. *C. r. Soc. Biol.,* **72,** 992-996; **73,** 326-327.

16. Henri, V. and Larguier de Bancels, J. Un nouveau type de temps de réaction. *C. r. Soc. Biol.,* **73,** 55-56.
    L'excitation provoquée par les rayons ultra-violets comparée avec les excitations visuelle et nerveuse, d'une part, et les reactions photochimiques, d'autre. Lois des phénomènes. *C. r. Soc. Biol.,* **73,** 328-329.

17. Henri, V. and Larguier de Bancels, J. Sur l'interprétation des lois de Weber et de Jost: recherches sur les réactions des cyclops exposées a la lumière ultra-violette. *Arch. de Psych.,* **12,** 329-342.

18. Holmes, S. J. Phototaxis in the Sea Urchin, *Arbacia punctulata.* *Jour. Animal Behav.,* **2,** 126-136.

19. Issel, R. Biologia neritica mediterranea. Recherche di etologia sull' Isopodo tubicolo, *Zenobiana prismatica* (Risso). *Arch. Zool. exp. gén.,* **51,** 479-500.

20. Jackson, H. H. T. A Contribution to the Natural History of the Amphipod, *Hyalella knickerbockeri* (Bate). *Bull. Wis. Nat. Hist. Soc.,* **10,** 49-60.

21. Jacobs, M. H. Studies on the Physiological Characters of Species. The Effect of Carbon Dioxide on Various Protozoa. *Jour. Exper. Zool.,* **12,** 519-542.

22. Jordan, J. Wie ziehen die Regenwürmer Blätter in ihre Röhren. *Zool. Jahrb., Abt. f. allg. Zool. Physiol.,* **33,** 95-106.

23. Jordan, H. Uber reflexarme Tiere. *Zeit. wiss. Zool.,* **101,** 116-138.

24. Kew, H. W. On the Pairing of Pseudoscorpions. *Proc. Zool. Soc. London,* 1912, 379-392.

25. Laubmann, A. L. Untersuchungen über die Hautsinnesorgane bei decapoden Krebsen aus der Gruppe der Cariciden. *Zool. Jahrb., Abt. f. Anat. Ontog.,* **35,** 105-159.

26. Mast, S. O. The Reactions of the Flagellate Peranema. *Jour. Animal Behav.,* **2,** 91-97.

27. Matisse, G. Les variations de l'activité motrice avec la température, et ses rythmes dans le temps. *Bull. Inst. gén. Psych.,* **12,** 177-202.

28. Moody, J. E. Observations on the Life History of Two Rare Ciliates, *Spathidium spathula* and *Actinobolus radians. Jour. Morph.,* **23,** 349-406.

29. Moore, A. R. Concerning Negative Phototropism in *Daphnia pulex. Jour. Exper. Zool.,* **13,** 573-575.

30. Moore, A. R. Negative Phototropism in Diaptomus by Means of Strychnine. *Univ. of Calif. Publications,* Physiol., **4,** 185-186.

31. Orton, J. H. An Account of the Natural History of the Slipper Limpet (*Crepidula fornicata*), with some Remarks on its Occurrence on the Oyster Grounds of the Essex Coast. *Jour. Marine Biol. Ass.,* **9,** 435-443.

32. Orton, J. H. The Mode of Feeding of Crepidula, with an Account of the Current Producing Mechanism in the Mantle Cavity, and some Remarks on the Mode of Feeding in Gastropods and Lamellibranchs. *Jour. Marine Biol. Ass.,* **9,** 444-478.

33. Parker, G. H. Nervous and Non-nervous Responses of Actinians. *Science,* N. S., **35,** 461-462.

34. Pearse, A. S. The Habits of Fiddler Crabs. *Philippine Jour. Science,* **7,** 113-133.

35. Polimanti, O. Studi di Fisiologia Etologica. II. Lo stato di immobilita temporanea ("morte apparente," "Totenstellung") nei Crostacei Brachiuri. *Zeit. f. allg. Physiol.,* **13,** 201-226.

36. Rynberk, J. von. Bausteine zu einer Segmentalphysiologie. *Ergeb. der Physiol.,* **12,** 660-764.

37. Sokolow, B.   Studien über Physiologie der Gregarinen.   *Archiv. f. Protisten-*
        kunde, **27**, 260-314.
38. Vieweger, T.   Recherches sur la sensibilité des infusoires (alcalio-oxytaxisme),
        les réflexes locomoteurs, l'action des sels.   *Arch. de Biol.*, **27**, 723-799.
39. Weymouth, F. W. and Richardson, C. H.   Observations on the Habits of the
        Crustacean *Emerita analoga*.   *Smithson. Misc. Coll.*, **59**, No. 7, 1-14.
40. Yerkes, R. M.   The Intelligence of Earthworms.   *Jour. Animal Behav.*, **2**,
        332-352.

LITERATURE FOR 1912 ON THE BEHAVIOR OF SPIDERS AND INSECTS OTHER THAN ANTS

C. H. TURNER

Sumner High School, St. Louis, Mo.

TROPISMS

1. *Thigmotropism.* Wodsedalek (110) deposited a brick in a vessel of water. On top of this brick he placed a few small pebbles of different sizes. On these pebbles he balanced another brick in such a manner as to form a graduated space between the bricks. A large number of the nymphs of *Heptagenia interpunctata* Say were placed in the water. In a short time, all of these may-fly nymphs were clinging, dorsal side downward, to the under side of the uppermost brick. A stone, with several attached nymphs, was placed in a tin vessel of water and the temperature of the water gradually raised. When the temperature had reached 42° C. the nymphs began to leave the stone, and by the time it had reached 45° all had departed. A stone so large that a portion of it would project above the water, was placed in an aquarium in which a chunk of ice was kept. In a short time all of the nymphs in the vessel were clinging to the submerged portions of the stone. The stone was then heated from above. As the stone gradually became hot, one by one the insects let go; but as soon as they were cool, they returned to the stone. Occasionally one of these returning nymphs would turn away just before reaching the stone, and other nymphs leaped from point to point along the rock, as though seeking a cooler place. Most of the nymphs spent their time roaming back and forth between the hot stone and the cool water. Wodsedalek noticed that, when given the opportunity, a nymph would wrap itself about a small pebble and become so rigidly fixed in that position that moulting was impossible. These experiments and observations caused Wodsedalek to conclude that strong positive thigmotropism is the most pronounced feature in the behavior of these may-fly nymphs.

C. F. Curtis Riley (79) is convinced that dragon-fly nymphs are positively thigmotactic and that this causes them to collect in groups.

W. P. Gee (32) claims that the young of the scale insect *Lecanium quercifex* Fitch are pronouncedly positively thigmotactic. A young nymph was placed upon its back and an unhatched egg applied to its upstretched feet. The insect at once . began to juggle the egg and continued to do so for nearly thirty hours. The egg hatched at the proper time; but the young insect had a hard time escaping from the grasp of the juggling scale.

2. *Phototropism.* Mast (57) states that the male fireflies studied by him always turned so as to face the glow of the female and then moved directly towards it.* He also noticed ˙ that the male continued to move in the direction of the glow even after it had ceased. Mast thinks the following mechanical explanation is justifiable. " If we assume * * * that there is in the male a specific response for the illumination of every surface of the eye; that is, that momentary illumination of the posterior surface is followed by a turning through 180° and then locomotion straight forward, the side of the eye by turning through 90° and then forward movement, the front of the eye by a forward movement alone, etc., it is not difficult to conceive all of these reactions to be purely mechanical reactions of the nature of unconscious reflexes." However, Mast does not consider these orientations tropisms in the sense of Loeb; for he writes: "Here we have a case in which it is clearly demonstrated that light does not act continuously in the process of orientation as demanded by Loeb's theories, a case in which it is also clearly demonstrated that a continuous action of the stimulating agent is not necessary to keep the organism oriented."

C. H. Turner (100) confined several of the mason wasps, *Trypoxylon albotarsus,* in wire cages and experimented on them with narrow bands of light, broad bands of light and cones of light. In some experiments direct sunlight and in others the beam of an electric projecting lantern served as the illuminant. Red, orange, blue and colorless lights were used. "As a rule, under the influence of a strong white light, these wasps would make active flights or else walk rapidly about." "When a light

* See Mast, under " Mating."

stimulus, no matter what the hue, tollowed one with a lesser brightness content, the wasps usually became active; but when it tollowed one of greater brightness content the wasps usually became inactive." "These responses were not tropisms, for the flights were pronouncedly random; there being no fixed relation between the direction of the movement and the rays of light."

By shifting an incandescent lamp from one end to the other of a glass dish and noting the responses of the scale *Lecanium quercifex* Fitch, Gee (32) thinks he has demonstrated that this scale is negatively phototactic.

According to C. F. Riley (79), dragon-fly nymphs are negatively phototropic to strong light.

During the year two papers, one by Hunter (43) and another by Hasebrock (39), have appeared which discuss the effect of the Roentgen rays upon the development of insects. The former experimented upon ticks, the latter upon butterflies. Hunter is convinced that the rays do not produce sterility.

3. *Geotropism.* Gee (32) arranged some thin sheets of cork in a vertical position and placed some scale insects, *Lecanium quercifex* Fitch, upon them. Invariably the insects crawled upwards, displaying, so he claims, positive geotaxis.

4. *Chemotropism.* Gee (32) tested the chemical responses of the scale insect *Lecanium quercifex* Fitch by placing, in the midst of a crowd of the scales, a drop of one of the following liquids: hydrochloric acid, nitric acid, ninety per cent. alcohol. In each case a marked negative reaction was produced.

SENSATIONS

Wodsedalek (110) is convinced that the nymphs of *Heptagenia interpunctata* Say cannot see small objects.

John Lovell (53) has published the results of some field work conducted to test Plateau's statement that "All flowers might be as green as their leaves without their pollination being compromised." Of the ninety-one green, greenish, brown, or brownish entomophilous flowers enumerated by Plateau only thirty per cent. were visited by bees, and some of these were conspicuous flowers. According to Lovell, in North America east of the 102nd meridian and north of North Carolina and Tennessee there are 1244 green or dull-colored flowers; of which 1021 are anemophilous or hydrophilous, while only 223 are entomophilous

or autogamous. Wind-fertilized flowers are small and usually greenish. The rose-colored flowers of *Gerardia purpurea* and flowers of the same species from which the corollas had been removed were placed near a bee-hive, but separated by a tumbler of water. Honey was placed in both. At first the bees collected from the perfect flower and neglected those from which the corollas had been removed. Bees were trained to collect from an unpainted board which was well supplied with honey. A blue slide, well supplied with honey, was placed on the ground three feet from the board. Honey was placed on a dandelion leaf which was growing three feet from the board and five from the blue slide. As soon as all of the honey had been removed from the board the bees began circling about it in widening curves. In twenty-five minutes five bees had begun to collect from the blue slide, but none had visited the dandelion leaf. Alongside of the dandelion leaf was placed an apple leaf that had been well supplied with honey. At the end of forty minutes one bee found the apple leaf. Bees were trained to collect from a board of the type used in the above experiment. Three feet from the middle of the board and forming an equilateral triangle with that point were two posts four and a half feet high. On the top of one post the investigator placed so much honey that it ran down the sides; on the top of the other he placed a scentless yellow *Helichrysum bracteatum* five inches in diameter. Three minutes after all of the honey had been removed from the board, three bees and one fly were on the flowers, but none was on the pole. The poles were now interchanged and a *Helichrysum bracteatum* only one inch in diameter was placed on the pole that had contained no flowers. Notwithstanding its changed position, the large and more conspicuous object received the greater number of visits. Bees were again trained to feed from a board of the type mentioned above. On the ground, nine feet from the board, Lovell placed a blossom of *Helichrysum bracteatum* containing honey. At the same distance on the opposite side of the board, he placed a red Astrachan apple leaf upon which he had put some honey. Several bees collected honey from the flower; but none visited the apple leaf. The observations recorded in the beginning of this paragraph and a series of experiments, of which the three just described are types, induced Lovell to form the following conclu-

sions: (1) Green flowers are not well adapted to entomophily. (2) As a rule they retain the power of self-fertilization. (3) The few insects that sparingly visit them usually belong to the less specialized families. (4) The fact that bees have been observed feeding on over-ripe or on decayed fruit, or on the glandular secretions of the vegetative organs of plants, or on the secretions of aphidae, or on greenish or brownish flowers, or on dull-colored receptacles which have contained sugar or sweet liquids, affords no evidence that conspicuousness is not an advantage to entomophilous flowers. (5) Any surface, whether bright or dull, on which there is nectar or honey will be visited by bees for stores after these liquids have once been discovered, but they will not be discovered as quickly on a surface which does not contrast in hue with its environment as on one which does. (6) When, under similar conditions, bees are given a choice between a conspicuous and an inconspicuous object they exhibit a preference for the former. This preference is sufficiently marked to account for the development of the color contrast in flowers. (7) As pointed out by Knuth, in the absence of control or comparative observations, the experiments and observations of Plateau on green or greenish flowers are fallacious and do not prove that "All flowers might be as green as their leaves without their pollination being compromised."

2. *Auditory.* Regan (76) has conducted a series of experiments to test the auditory powers of *Liogryllus campestris.*

EMOTIONS

Stubbs (94) discusses fear in insects.

Wodsedalek (108) arranged a large number of small aquaria, each containing a single nymph of the may-fly *Heptagenia interpunctata* Say, in different parts of the same room. Six of these specimens were roughly handled three times a day; three were disturbed once daily; three, once in three days; and six, not at all. The specimens that had been roughly handled three times a day made agitated movements whenever the hand of the investigator was passed over the water, and, in some cases, as soon as he approached the aquarium. Such behavior was almost never exhibited by nymphs that had been handled only once a day or less. It seems that the investigator is justified in concluding that these are fear reactions. "These results seem

to show that the nymphs formed few, if any, associations with pain resulting from a single daily disturbance. * * * In the forms disturbed several times a day, however, even after making liberal allowance for accidental movements, there remains abundant evidence that the nymphs learned to associate my presence with discomfort."

MATING INSTINCTS

S. B. Oliver (67) reports some abnormal matings of insects; S. B. Doten (24) discusses the relation of food to the reproductive activities and the longevity of certain hymenopterous parasites, and C. H. Turner (99) gives a photograph of the copulation of *Ammophila abbreviata*.

Robert Matheson and C. R. Crosby (58) observed, on three different occasions, *Caraphractus cinctus* Walker copulating beneath the surface of the water.

In a paper containing some valuable data on the longevity of saturnid moths, Phil and Nellie Rau (75) state that mating has no effect on the duration of life of the male Cecropia moth; but that, in six different lots, the unmated females lived longer than those that succeeded in mating.

According to Wodsedalek (109), on the day of emerging, the female of the museum pest *Trogoderma tarsale* Melsh avoids the male. On the following day she is submissive. At that time the male caresses the abdomen of the female with his antennae and then suddenly turns and brings the tip of his abdomen in contact with hers. These insects are both polyandrous and polygamous.

During the year two investigators, F. A. McDermott (54, 55) and S. O. Mast (57), working independently, have decided that the photogenic function of fireflies is a mating adaptation. Both of McDermott's papers are corrections of and additions to a former paper;* Mast's paper discusses in detail, the mating of *Photinus pyralis*. The following paragraph contains an epitome of Mast's paper.

Late in the afternoon, but while it is yet light enough to see, both sexes of the fireflies emerge from their subterranean crevices. The females climb blades of grass, or other uprights, and

* McDermott, F. N. A Note on Light-Emission of Some American Lampyridae. *Canad. Entom.*, 1910, vol. 40, pp. 357-363.

rest thereon. The males fly leisurely about, at a height of from one to two meters, emitting, at regular intervals, flashes of light. If the male glows within five or six meters of the female, she twists her body so as to have the luminous surface of her abdomen face the male and then glows in response. The male then turns directly towards the female, glows again and moves directly towards her, glowing intermittently as he flies. To each glow the female responds in kind. Arriving near the female, the male alights, runs about in an excited manner and glows frequently. Sooner or later the antennae of the excited insects touch and then the fireflies mate. Immediately the glowing ceases. When females were enclosed in air-tight glass jars, the males found them readily. This caused Mast to conclude that smell plays no part in bringing the insects together. Two sealed jars containing male fireflies and one containing females were placed on the ground. The males of the two jars were always in plain view of each other; but, by means of an opaque screen, the females were hidden from first one and then the other of the sets of males. The males exposed to the females glowed repeatedly; but the others glowed only after long intervals. This caused him to conclude that the males do not respond to the glow of other males. Other experiments showed that the female will respond to any intermittent glow, even when produced by artificial means; but the males respond only to the glow of the female.

NEST-BUILDING AND MATERNAL INSTINCTS

Cosens (22) gives some interesting information about the galls of numerous insects, and Casteel (16) describes in detail the manipulation of wax scales by the honey bee.

Hungerford and Williams (42) describe the nests of the following hymenopterous insects: *Pogonomyrmex occidentalis* Cress., *Chlorion caeruleum* Drury, *Bembex sayi* Cress., *Trypoxylon texense* Sauss., *Crabo interruptus* St. Fargo, *Odynerus annulatus* Say, *Loxostege stiticalis*, *Odynerus geminus* Cress., *Odynerus foraminatus* Sauss., *Polistes variatus* Cr., *Halictus occidentalis*, *Anthidium maculiforus* Smith, *Dianthidium concinnum*, *Dianthidium curvatus* Smith, *Megacheli Sp.?*, *Melitoma grisella* Ckll., and Porter, *Anthophora occidentalis* Cress., and *Ammophila sp.?* To students of the behavior of the hymenopterous insects, all of

the data will prove of interest. The authors' description of the nest-building of *Odynerus annulatus* Say is intensely interesting. In digging its nest this species moistens the soil with water, removes a small portion of the moistened soil and with it begins to construct a turret around the spot. Some more water is added and another small portion of the soil is removed and added to the turret. This is repeated over and over again and the turret, which is smooth on the inside and rough on the outside, grows apace. As the work advances only a part of the pellets removed from the burrow are built into the turret. The others are carried a distance of from four to six feet and dropped. Whence comes the water to moisten the soil? The wasp brings it, in her mouth, from a nearby lagoon. These investigators contribute additional proof, if such be needed, of the tool using instinct of the Ammophilae. They found one species of Ammophila using a stick to tamp the dirt on its burrow and another species using the tibia and tarsus of a small locust for the same purpose.

In his new book, Comstock (21) describes the webs, and in some cases the web-making activities of a large number of spiders, and, in a second contribution (20) he discusses, in the following manner, the probable evolution of the spider web. Some spiders in constructing their webs use several distinct kinds of silk, for the elaboration of which complicated spinning organs have been evolved. At least seven different kinds of silk are spun by spiders. From the few silken strands used by Pholcus to fasten her eggs together to the dense sheets used by others to construct elaborate egg-cases, silk in some form is used by all spiders in caring for their eggs. This was probably the primitive use of silk. Spiders living in burrows strengthen them by means of silk; some construct silken covers for the burrow and others build silken turrets. The most important step towards real web building was acquiring the habit of spinning a drag-line. "The step from drag-line to web is not a great one. A spider spinning a thread wherever it goes would make a web if, by chance, it moved about in a limited space, as in some nook in which it had taken up its abode. In such a web insects would be trapped, and thus might arise the habit of building webs for the purpose of trapping insects." The simplest webs are irregular and constructed out of dry silk like that used for

the drag-line. The web of Pholcus is a good example. The webs of the sheet-web builders are constructed of this kind of silk; but they have a more or less definite form. Slightly higher than these and constructed of the same kind of silk are the webs of certain members of the Agelenidae, which have a definite shape and a funnel-shaped retreat. These webs of dry silk simply impede the progress of the insect and enable the spider to capture them. To assist in holding the snared insects, many spiders secrete a viscid silk. Among the webs constructed in part of viscid silk there are evidences of evolution. The webs of the Theridiidae are almost as simple as those of Pholcus; but the inmate swathes a viscid fluid about its prey. Other spiders construct viscid bands or viscid threads in their webs. Of these webs there are two types; one in which the portion constructed of dry silk is comparatively generalized and in which the viscid silk is supported by a specialized band; and another in which the foundation of dry silk is highly specialized and in which the structure of viscid silk has remained comparatively simple. In each class the webs may be arranged in a series indicating the path of evolution. Since this viscid fluid is produced by the lobed glands in the Theridiidae, by the cribellum glands in the Cribellatae, and by yet other glands in other spiders, Comstock claims that this viscid fluid has arisen, independently, at least three times. In addition to describing the web-building behavior of spiders, Comstock gives a key for recognizing groups of spiders by their webs.

Weiss (106) describes the egg-laying of *Lixus concavus*.

Matheson and Crosby (58) describe the oviposition of *Limnodytes gerriphagus* Marchal and *Caraphractus cinctus* Walker.

Pierce and Holloway (73) state that *Chelonus texanus* Cress. deposits its eggs in the egg of the host insect; but that the parasite emerges from the larva which develops from the egg.

FOOD-PROCURING AND DEFENSIVE INSTINCTS

Campion (14) describes the feeding habits of the scorpion flies; Cockerell (17) of *Dysdercus mimus* Say; Hungerford and Williams (42) of the young of *Ammophila* sp.?, *Chlorion caeruleum* Drura, *Trypoxylon texensis*, *Crabo interruptus* St. Fargo, *Odynerus annulatus* Say, *O. geminus* Cress., *Halictus maculifrons*, *Dianthus concinnum;* Moore (62) of a large number of

caterpillars; Riley (80) of dragon-fly nymphs; Turner (100) of *Trypoxylon albotarsus;* Weiss (106) of *Lixus concavus;* Wodse-dalek of the nymphs of *Trogoderma tarsale* Melsh (109) and of *Heptagenia interpunctata* Say (110).

Two investigators, Sladen of England and Casteel of this country, have contributed articles on the behavior of the honey bee in pollen collecting. F. W. L. Sladen (87) says that the pollen is gathered directly upon the metatarsal brushes. By scraping the inner sides of the metatarsi the pollen is compacted in the corbiculae. In spite of Cheshire's statement to the contrary,* Sladen asserts that there is no crossing of the legs.

At the beginning of his article, Casteel (15) emphasizes the well-known fact that bees do not combine pollen collecting with honey gathering. Following that statement comes a detailed account of how pollen is collected. In moving about among the stamens, some pollen clings to the hairs of the body and of the legs; but the greater part of the pollen is collected by the mandibles and tongue. The pollen collected by the hairs of the body and of the legs is dry; that collected by the mouth-parts is moistened with honey supplied by the mouth. The first pair of legs collects the dry pollen from the head region and the moist pollen from the mouth-parts. The second pair of legs removes the pollen from the ventral side of the thorax and receives that which has been collected by the first leg. The third pair of legs collects the pollen from the abdomen and receives that which has been collected by the second pair of legs. The third pair of legs now scrape the pollen from the the combs and sides of one into the corbiculae of the other. The moisture which has been supplied by the mouth causes it to adhere. In unloading the bee grasps one edge of the cell with her forelegs and arches her abdomen until its posterior edge rests on the opposite side of the cell. The middle legs then shove the pollen mass from the third legs into the cell. Usually another bee enters the cell, breaks the pellets with her mandibles and tamps down the mass in the bottom of the cell. She probably adds more fluid.

C. H. Turner (98) found some orphan *Polistes pallipes,* that he had raised from the larval stage, so tame that they would accept honey or insect larvae when offered to them on glass

* Bees and Bee Keeping, vol. I, p. 132.

rods, in forceps, or even upon the fingers. Belt writes: "A specimen of *Polistes carnifex* was hunting for caterpillars in my garden. I found one about an inch long and held it up towards it on the point of a stick. It seized it immediately, and commenced biting it from head to tail, soon reducing the soft body to a mass of pulp. It rolled up half of it into a ball and prepared to carry it off." Turner observed that the behavior of *Polistes pallipes* is quite unlike this. "Lepidopterous larvae captured for food are not stung. Grasping the caterpillar with her fore feet, the wasp rotates it on its longitudinal axis and gradually elevates it while she malaxates its posterior end until her jaws are filled with a ball of pulpy matter. The remainder of the insect is dropped."

Croft (23) observed a notodontid attacked by a wasp, and E. O. Essig (25) has discussed several natural enemies of the citrus plant louse.

To test the protective value of vapors emitted by certain bugs, Girault (34) performed a number of experiments. Certain bugs were confined to homoepathic vials for from three to twenty-four hours. They were then removed and some insect corked up in each vial. Control insects of the same species were placed in clean vials. Ants, beetles, plant lice, etc., were tested in this manner. The odors of certain bugs had no effect on the species studied; but the odor of others caused stupefaction, convulsions and, in some cases, death. Girault does not claim that these experiments settle the protective value of these odors; but that they demonstrate that the vapors emitted by certain bugs are highly noxious to various forms of insect life.

SOUND PRODUCING ACTIVITIES

Butler (12) describes the stridulation of some British bugs.

Recently two investigators, Omensetter and Stephan, have produced papers on the speech of insects. Omensetter's paper (68), which seems to be a compilation, describes the sounds produced by many insects belonging to the Lepidoptera, Orthoptera, Hymenoptera, Coleoptera, and Neuroptera. He writes: "That pleasure or pain makes a difference in the tones of vocal insects is not improbable, but the organs of hearing are not fine enough to catch all their different modulations."

In his papers Stephan (91, 92) confines himself to the Lepi-

doptera. Aeronia produces sound by striking one wing against the other. *Cozistra membranacea* produces sound by means of its wings. *Parnassius apollo* L. produces tones by rubbing the tibia against the hind wings. The male *Thecophora fovea* Tr., when flying, makes sounds by means of an uncovered small cavity in the middle of the hind wing. *Nyctipo hieroglyphia* Dr., *Anisoneura sphingoides* Fld., and *Potamorpha manilia* Cr. produce sounds by rubbing the narrow concavity of the fore-wing over an enlarged structure on the hind wing. The male *Lymantria monacha* L. makes a noise so loud that it can be heard, when held at arms' length, in a closed fist. In stressing the mode of sound production used by the death's head moth, he reminds us that, in 1737, Reaumer claimed that the sound was produced by rubbing the proboscis upon the inner edge of the base of the palpi; that, in 1867, Landois stated that it was produced by rubbing the inner surface of the palpi upon the proboscis; that Wagner, in 1838, and Landois, in 1875, claimed that in front of the stomach there is a bladder which usually is filled with air, and that the expulsion of this air across the proboscis causes the tones. This explanation is supported by the fact that compression of the dead body of a death's head moth that has not become rigid will produce the sound. Stephan seems to support this last interpretation. Several witnesses should be sufficient to establish this matter; but, to a student of insect behavior, this method of sound production is certainly unique; for he has come to believe that the strident sounds of insects are always instrumental and never vocal.

LETISIMULATION*

C. F. Riley (79) states that many of the dragon-fly nymphs studied by him letisimulated.

Wodsedalek (109) discovered that the larvae of the museum pest *Trogoderma tarsale* Melsh letisimulates when disturbed. The feint usually lasts from a few seconds to half a minute. The adults, when disturbed, feign death for a much longer time; among them the average is thirty seconds, but it may continue for fifteen minutes.

---

* This word, which has not yet come into common use, was first used by Weir, in 1899, in his book on "Dawn of Reason," page 202, to designate the death-feigning behavior of animals. Now that stress is being placed on animal behavior, it seems to me that the term should be revived.

According to Wodsedalek (108), rough handling of the ephe-
meridae nymphs *Heptogenia interpunctata* Say produces leti-
simulation. The time of the feint varies from a fraction of a
minute to fifteen minutes. The average is between two and
three minutes. Prolonged stroking of the nymph on the sternum
or on the ventral side of the abdomen will prolong the feint.
By such means a feint has been prolonged for an hour. A touch
with a smooth object tends to prolong the spell; a tap with a
sharp one arouses the insect.

Gee and Lathrop (31) describe three methods of inducing
this form of behavior in *Contrachelus nenuphar* Herbst: (1)
dropping them from a height in the air; (2) compressing, at
short intervals, the lateral surfaces of the abdomen and thorax;
(3) grasping the insect between the thumb and forefinger and
suddenly blowing upon the ventral surface of the abdomen.
Two distinct postures are assumed by the letisimulating indi-
viduals. In one type the individual draws the thoracic appen-
dages closely against the ventral surface of the body. The first
pair of legs extend forwards and are pressed against each side
of the proboscis. The closely flexed second and third pairs of
legs are held securely against the ventral side of the abdomen.
In the other type the legs are folded closely together and held
somewhat at right angles to the line of the body. The tarsi of
the first and of the second pairs of legs are drawn tightly against
the tibia; but, in the third pair, they are held approximately
parallel to the ventral surface of the thorax. In the first type
the pose resembles the attitude of insects that have been starved
to death or killed by slow poison. These investigators suc-
ceeded in causing one individual to letisimulate fifty-three times;
but, after the first few times, the duration of each successive
feint was gradually reduced until the animal would not leti-
simulate at all. To test the influence of temperature, letisimu-
lating individuals were placed in a glass and held over a flame.
In every case the individual quickly recovered. This is unlike
DeGeer's experience with the beetle *Anobrium pertinax;* which,
he claims, could be roasted over a slow fire without recovering.
Gee and Lathrop find that a low temperature increases the
duration of the death feint, thus agreeing with Fabre's work on
Caponoides tenebrinicnis and Holmes' work on *Ranatra.* It was
found that letisimulating individuals, when placed in an atmos-

phere saturated with ether, chloroform, or carbon dioxide, re-
cover at once. One by one, the appendages of eight letisimu-
lating individuals were removed. With two exceptions, these
showed no signs of recovering from the feint until several min-
utes after the operation. The abdomens were clipped from
several individuals; slight twitchings of the tarsi were the only
movements produced by the amputation. Seven letisimulating
individuals were decapitated with sharp scissors. Immediately
the legs relaxed and righting movements were made. These
investigators remind us that letisimulation occurs in almost all
orders of insects; that Holmes observed it in an amphipod
crustacean, and Andrews in the crayfish. It occurs rarely
among fishes and to some extent in the amphibia. It occurs
in several reptiles and birds and in a few mammals. Gee and
Lathrop agree with Holmes and with the Severins that this
form of behavior has developed out of thigmotactic propensities.

DISEASE SPREADING INSTINCTS

W. E. Britton (5, 6), C. T. Brues (10) and J. H. Paine (70),
have published helpful popular articles on the relation of in-
sects to diseases.

Jennings (45) has discussed the method of controlling the
mosquitoes of the tropics, and W. E. Britton (6) the methods
of combating those of our Connecticut coast. The methods
advocated are well known to entomologists.

C. T. Brues (11) gives a tabulated list of the diseases spread
by insects and of the insects that spread them. He gives the
following reasons for believing that infantile paralysis is caused
by some insect: (1) the sporadic occurrence of the cases is
not easily explained on the basis of ordinary contact infection;
(2) the seasonal distribution of the disease, showing the largest
number of cases during the warmer months; (3) its failure to
spread rapidly where many children are in close contact; and
(4) the characteristic rural nature of the disease. He gives
reasons why it is improbable that this disease is spread by
either the mosquito, the stable fly, the horn-fly, or fleas. He
suggests that it is spread by the tick; but he could find no
conclusive proof of this.

C. H. T. Townsend (96) thinks that verruga fever is spread by
ticks in the same manner as the Rocky Mountain spotted fever.

According to Wm. Moore (64), "One of the most important and interesting problems in economic entomology is the rôle played by ticks in the spread of certain diseases and how these ticks may be destroyed." "In South Africa it is not one tick and one disease which must be dealt with, but a number of ticks producing a number of different diseases." The blue tick causes Texas cattle fever and spirochaetosis; the Bont tick induces heart-water disease in sheep, goats, etc.; the dog tick spread malignant jaundice among dogs; the brown tick transmits East Coast fever and gall sickness to cattle and may transmit Texas cattle fever; the Cape brown tick causes East Coast fever; the black pitted tick transmits East Coast fever and gall sickness and may spread spirochaetosis; the red tick is a carrier of East Coast fever, gall sickness and the biliary fever of horses. Moore discusses the life-histories of all of these ticks and gives methods of combating them. What he considers the most successful remedy is weekly dipping of the animals in a sufficient amount of the following mixture: three pounds of soft soap, one gallon of kerosene, four ponds of arsenite of soda, and four hundred gallons of water.

Frederick Knab (47) has well said: "The study of the rôle of blood-sucking insects in the transmission of diseases is a recent one, and it is still to a large extent vague and chaotic. Its teachings are not only built up largely on hastily collected and faulty data, but they are replete with errors. Many of the investigators not only have lacked the necessary knowledge of biology, but the mastery of detail, along with a broader view, which is eminently necessary in such work. Since the discovery that certain blood-sucking insects are the secondary hosts of pathogenic parasites, nearly every insect that sucks blood, whether habitually or occasionally, has been suspected or considered a possible transmitter of disease. * * * In order to be a potential transmitter of human blood-parasites, an insect must be closely associated with man and normally have opportunity to suck his blood. It is not sufficient that occasional specimens bite man." There is "a certain class of blood-parasites and transmitters which apparently do not conform to the principles laid down above. One class are the diseases transmitted by ticks, where the parasites are directly transmitted from the tick host to its offspring, and where, for this reason,

the insect remains a potential transmitter for a very long period. Another class are the trypanosomes which apparently thrive in a number of different vertebrate hosts and may be transmitted from cattle or wild beasts to man. But the observations on this point are by no means conclusive and it is quite possible, as has been repeatedly suggested, that a number of organisms, different but indistinguishable, are involved. It may prove that revision of data, from the present viewpoint, may materially alter our conceptions on the subject."

PARASITISM

Knab (48) reports a fly that is parasitic on man.

Girault (34) records some simple experiments which he performed with the human body louse.

Matheson and Crosby (58) discuss the habits of three hymenopterous egg parasites.

Ewing (27) gives a classification of parasites that covers two octavo pages. In the Acarina he finds evidence that parasitism has arisen in the following three ways: (1) by predaceous forms beginning to prey upon forms that are larger than they; (2) by scavengers passing from feeding on dead bits of animal and of plant tissues to feeding on the same tissues attached to a living organism and thence to feeding on the living organism; (3) by forms originally adapted for sucking the juices of plants, transferring their operations to animals. He gives a list of parasites and their hosts, and, in tabulated form, he records the duration of life of many mites after being removed from the body of their host.

LOCOMOTION

Bervoets (3) has published a short article on the flight of insects, and Collinge (19), a short note on the locomotion of the young of *Pulvinaria vitis* var. *ribesiae*.

H. W. B. Moore (63) describes the locomotion of a large number of caterpillars.

Matheson and Crosby (58) describe the behavior of three different species of American hymenoptera which swim, submerged in water, by means of their wings. These species are: *Hydrophylax aquivolans* M. and C., *Limnodytes gerriphagus* Marchal and *Caraphractus cinctus* Walker.

During the year Severin and Hartung (84) set free near Hono-
lulu 2,000 male Mediterranean fruit flies which had been marked
by removing a portion of a leg.   Light traps for recapturing
them were placed in definite situations.   These investigators
found that the wind had a marked influence both on the direc-
tion of the flight and on the distance flown.   In time of calm,
the flies flew in all directions, but when the wind was blowing,
the flies drifted with it.   In no case did they attempt to orient
themselves against even the slightest breeze.

H. Osborn (69) expresses some thoughts on the flight of
insects; which reflections he claims are suggestive rather than
exhaustive.   In the usual explanation of the flight of insects,
the mechanism is considered essentially a plane with a rigid
anterior border, a flexible hinder border and a vertical move-
ment.   At each downward stroke of the wings the air in escap-
ing backwards and upwards propels the insect forward.   Aside
from the directly forward flight, insects are able to hover and
even to fly backward.   Osborn rightly concludes that this hover-
ing and this backward flight are not explained by the above
formula.   He offers the following explanation of hovering and
backward flight.   There is a forward and backward movement
of the wings which permits the angle a wing makes with the
body to be varied from 90° to 45° or 30°.   By this device the
rigid portion of the anterior border of the wing is shifted so that
the flexible apical and posterior margins have a different extent
and must present a varying pressure upon the air.   This rota-
tion will allow varying degrees of forward and backward pres-
sure.   The attitude assumed by the wings of many insects after
death is evidence that such a mechanism actually exists.   The
extent of the rotation differs in different groups of insects.   The
shape of the wing functions also.   Broad winged insects neither
hover well nor fly backwards well; while narrow winged hexa-
pods excel in both styles of flight.

MISCELLANEOUS INSTINCTS

In years that are past so many abortive attempts have been
made to find a true queen of the common northern termite
that many had come to believe there were no true queens in our
species.   This year, however, such a queen has been found

and the credit goes to T. E. Snyder (90). It was found deep
in the ground.

Mace (56) has conducted experiments to test the influence of
weather upon the honey bee. The hive was weighed from day
to day and the results compared with the weather conditions.
He arrived at the following conclusions: (1) high winds cause
great loss among the colonies; (2) during the honey flow in
the early part of the season, weak colonies should have their
brood space contracted so as to conserve all of the heat pos-
sible; (3) as soon as the brood combs are well covered with
bees and the weather is fine, the supers should be put on and
covered up warmly.

Cannibalism. According to Weiss (106), *Lixus concavus*, the
rhubarb cuculio, lays a great many eggs in the stem of *Rumex
crispus* and most of these hatch; yet, except where more than
one stem is attached to the same root, not more than one larva
is ever found in a root. The cannibalistic habits of the larva
explain this. As soon as a larva hatches it eats out a little
chamber above the egg cavity and then proceeds to mine an
irregular passageway to the root. Any eggs encountered on the
way are devoured. In the root it excavates a cavity and con-
tinues to feed until full grown. Any belated larva that arrives
at the roots is devoured by the cannibal domiciled there.

C. F. Riley (79) reports that dragon-fly nymphs are can-
nibals.

By restricting them to a honey diet for a few days, Turner
(98) caused a small colony of *Polistes pallipes* to display can-
nibalistic habits. "Bit by bit, they removed the cap from a
pupal cell, decapitated the inmate and ate the contents of its
thorax."

Ecology. Shelford (85), as a result of field studies extending over
several years, concludes that the land animal life of a place is
largely determined by the kind of vegetation growing there.
Following Cowles' lead, he recognizes the following stages in
the evolution of a wood: (1) the cottonwood stage; (2) a
transition between the cottonwood stage and the pine stage;
(3) the pine stage; (4) transition between the pine stage and
the oak stage, or mixed pines and oaks together with open
spaces in the oak area; (5) the black oak stage; (6) the red

oak stage (the red oak associated with the black oak and white oak in the earlier stages, and with shag-bark hickory, in the later stages); (7) the beech and maple stages. In each of these plant communities the animals live in five or more less distinct strata: (1) beneath the ground (subterranean stratum); (2) at the surface of the ground (ground stratum); (3) herbaceous vegetation, low shrubs, etc., (field stratum); (4) shrubs and young trees (shrub stratum); (5) trees (tree stratum). In considering different communities like strata should be compared. Many animals invade several strata; they should be classified primarily in the stratum in which they breed and secondarily in the stratum or strata in which they feed or forage. Shelford gives a rather exhaustive discussion of both communities and strata, and gives tables showing the distribution of animal life in both. The following epitome of his conclusions will be of interest, not only to students of insect behavior, but to all field zoölogists. (1) The development of a forest on sand or other mineral soil is accompanied by an almost complete change of animal species and probably by a complete change of animal mores. (2) Forest development is accompanied by marked changes in the soil and in physical factors; animal distribution is more closely correlated with differences in physical factors than with the species of plants. (3) For animals dwelling in the soil, the moisture equivalent or the wilting coefficient for a standard plant is the best index of the moisture available to the animals. (4) The evaporating power of the air is probably the best index of the conditions of the atmosphere. (5) The rate of evaporation, temperature, etc , varies much in different communities and in different strata of the same community. (6) Land animals are comparable to small non-rooted plants. (7) The succession of all of the animals of a forest community is comparable in principle to that in ponds; it is due to an increment of changes in conditions produced by the plants and the animals living at the given point. (8) The various animal species are arranged in these communities in an orderly fashion and the dominating animal mores are correlated with the dominating conditions. (9) Taxonomic species usually have the same mores, although the same species often has different mores under different conditions, and different species may have the same mores. (10) Species and mores are not synonymous.

(11) Ecology considers together mores that are alike or similar in their larger characters.

Hibernation. At a depth of about three inches, Blaisdell (4) found sixty-four specimens of the tiger beetle *Cincindela senilis* hibernating beneath a stone. The mouths of the burrows were at the edge of the rock, and at each there was a little pile of dirt that had been excavated in digging the burrows. Each burrow had one main gallery with branches leading distinctly to the edge of the stone. The branches that did not end blindly were closed with dirt. The main gallery, which was not more than half an inch below the surface, came to the surface at certain points. Blaisdell thinks the gallery became community property through an accident.

Mayer (59) discusses the hibernation of *Pyremeis atalanta*.

Migrations. Grossbeck (37) discusses the migration of the Argillacea of Alabama.

Moulting. Ewing (26) has the distinction of being the first to describe the moulting of our common red spider. The larva moves its body back and forth and sidewise. Suddenly the skin of the dorsal surface bursts just back of the scapular groove. In an instant some of the bristles of the thorax are released and the eyes of the emerging nymph burst into view. Following a series of side movements, the hindmost legs are extended laterally and slightly anteriorly. The body wriggles for a moment, then the anterior portion begins to be withdrawn from the old larval skin. The movement is slow until the first pair of legs appear, then the nymph suddenly pulls loose from the anterior portion of the old skin and walks out of the posterior portion. The total time consumed is only four minutes.

Turner (98) describes an abortive attempt of a pupa of *Polistes pallipes* to moult.

Phosphorescence. Green (35) describes the phosphorescence of the beetle *Harmatelia bilinea*.

See McDermott and Mast, under "Mating."

Singh and Maulik (86) found that the so-called phosphorescence of the fireflies would affect the photographic plate through wood, dark brown leather, black paper, or flesh; but that it would not affect the plate through glass. Hence they

conclude: "The light of this insect cannot, therefore, be taken as phosphorescent.   It may be, perhaps, premature to conclude that some rays emitted by these insects are X-rays, but it may be safely asserted that these rays are at least similar to the X-rays and ultra-violet light in so far as they may render certain opaque media transparent and are intercepted by glass."

Homing.   On departing from a place that it is likely to revisit, *Polistes pallipes* makes a flight of orientation.   This has caused Turner (98) to conclude that associative memory guides this wasp home.

Respiration.   Babak (1) discusses the breathing of *Culex*.

Brocher (7, 8, 9) devoted about four years to the study of the respiration of certain aquatic hymenoptera.   He paid especial attention to *Elmis aeneus*.   He finds that this species obtains the necessary oxygen, not from the air direct, but from submerged plants.   Bubbles of air obtained from the plants cling to their bodies.   Brocher describes at length the organs by means of which this mode of respiration is carried on.

MEMORY AND LEARNING BY ASSOCIATION

Turner (101) noticed a digger wasp trying to drag a spider to her nest.   In her path she encountered a tall fence, over which, on account of a horizontal scantling, she found it impossible to drag her burden.   Turning about, she dragged the spider along the fence until the corner of the yard was reached.   Then she passed through the pickets of the front fence to the outside.   Depositing her burden on the ground, she made a flight of orientation and flew off to the nest.   Returning, she dragged the spider along the ground towards the nest, and, after overcoming numerous minor hindrances, she succeeded in depositing the spider in her nest.   The line by which she finally reached the nest made an angle of about 45° with the line along which she originally attempted to drag the spider home.   The investigator concludes: "The behavior of this wasp does not harmonize with the theory that the movements of wasps are tropisms in the sense the term is used by Loeb; nor is it apparent how it can be the result of what Thorndike calls 'trial and error' movements.   Her whole behavior is that of a creature

struggling against obstacles to attain a certain known place in a known environment."

Two investigators, Szymanski and Turner, have conducted experiments to test the ability of the common roach to form new associations. The general method used was practically identical, not because one had copied from the other, but because each had been inspired by Yerkes' work on mice. A bottomless glass pen, containing two compartments, one light and one dark, was placed on a specially arranged electrical shocking platform. In the lighted division of the pen marked roaches were placed one at a time. Following its instinctive tendency, an untrained roach would rush into the dark chamber. Immediately an electric shock was given, which caused the roach to return to the lighted portion. In the lighted compartment it would become restless and, sooner or later, it would enter the dark section. There it received another shock which caused it to return to the light. Every time it reëntered the dark chamber it was driven out by means of electric shocks. Soon it would hesitate and later turn back when the dark chamber was reached. Indeed, after a little training, the roach would resist attempts to shove it into the dark chamber. When the roach had made ten successive refusals to enter the dark chamber, the experiment was concluded for that day; to be repeated on the following and on a long series of successive days.

Szymanski (95) confined his experiments to larval male roaches of about the same age. Most of these were used in their normal condition; but from a few the antennae were amputated. Based upon their ability to form associations, Szymanski divides his roaches into three classes: (1) those that make rapid progress and fatigue slowly; (2) those that make rapid progress and fatigue rapidly, and (3) those that make slow progress and fatigue rapidly. Marked individual differences were noted in the length of time that they retained the acquired habit; but no relation was evident between the degree of permanency of the acquired habit and the number of shocks necessary to instill it. Although the training influences the creature for only a short time, the influence of it is latent. This is proven by the rapidity with which roaches that have once been trained relearn the habit. It is possible

to establish the habit in animals from which both antennae have been amputated.

Turner (97) experimented with adult roaches of both sexes, larvae of several different ages, and roaches from which the antennae had been amputated. This investigator agrees with the conclusions reported in the above paragraph and adds: "Generally speaking, male roaches learn more rapidly than female and young roaches are more apt than adults, but there are marked individual exceptions to this; roaches that have acquired the habit of refusing to enter a specific dark place do not lose that habit when they moult; during sickness and just prior to death, the retentiveness of the roach is much impaired." To test the meaning of this refusal to enter the dark chamber, Turner conducted the following experiment. A bottomless pen, containing one dark and one lighted chamber, was placed on a piece of white cardboard. A roach that had thoroughly learned to avoid the dark chamber and which had just been tested to see if the habit was well fixed, was placed in the lighted compartment of this pen. As soon as its meanderings brought it to the entrance of the dark room, it would enter. Immediately the roach was returned to the lighted compartment of the pen which was resting on the shocking board. In that pen it could not be induced, even by gently shoving it, to enter the dark section. After many repetitions of this experiment had demonstrated that normal roaches almost invariably react in this manner, the investigator concluded: "To my mind this test is a conclusive proof that the change in behavior of these insects is not due to a physiological reversal of the phototropic responses of the roaches, but a case of learning, by experience, to avoid a specific dark place because of certain disagreeable experiences connected with it."

By means of experiments, Wodsedalek (108) has been able to induce may-fly nymphs to form three new kinds of associations: (1) they were induced to increase the distance they would swim towards a stone, even when they must swim against the rays of light; (2) by means of rough handling, they were caused to exhibit fear (these fear reactions are discussed under "Emotions."), and, (3) by a method about to be described, they were trained to make new responses to food. Bits of algae were

presented to a nymph in forceps. After the insect had secured a hold, the forceps were gently withdrawn, thus inducing the nymph to follow. Later, a piece of alga was held near the nymph and, when the hungry creature attempted to secure the food, the forceps were gradually withdrawn. This caused the insect to follow the food. After being subjected for four weeks to such experimenting, many of the nymphs learned to swim considerable distances towards the food, and some would even swim towards the investigator if he made his appearance at one end of the aquarium when they were at the other. After two and a half months of such experience as soon as the experimenter appeared, the majority of the nymphs would swim towards him and claw against the side of the aquarium, and one nymph would even climb a stone and reach up into the air after food. Untrained nymphs never behaved in this manner. Wodsedalek feels that these three types of experiments demonstrate (1) that nymphs can be trained to respond positively to objects even in a lighted environment, (2) that they can learn gradually to inhibit their usual negative responses to light and proportionately reinforce their reaction to an object against the rays of light and in the presence of that object, and (3) that they can learn to associate the investigator's presence with food.

REFERENCES

1. Babák, E. Zur Physiologie der Atmung bei Culex. *Int. Rev. d. Ges. Hydrobiol. und Hydrogr.*, Leipzig, 1912, 81-90.
2. Benick, L. Zur Biologie des *Necrophorus vestigator* nebst Beschreibung der Larve und Nymphe. *Entom. Blätter*, Cassel, **8**, 197-203.
3. Bervoets, R. Note préliminaire sur le vol des insectes. *Ann. Soc. Entom. de Belgique*, **56**, 348-350.
4. Blaisdell, Frank S. Hibernation of *Cincindela senilis*. *Entom. News*, **23**, 156-159.
5. Britton, W. E. The Rôle of the House Fly and Certain Other Insects in the Spread of Human Diseases. *Pop. Sci. Mo.*, **81**, 36-49.
6. Britton, W. E. The Mosquito Plague of the Connecticut Coast Region and How to Control It. *Conn. Agri. Ex. Station*, New Haven, Bull. 173, 14 pp.
7. Brocher, Frank. Recherches sur la respiration des insectes aquatiques adultes. Les Elmides. *Ann. Biol. Lacustre*, **5**, 136-180.
8. Brocher, F. Recherches sur la respiration des insectes aquatiques (imagoes) Nepe, Hydrophile, Notonecte, Dyticides, Haemonia, Elmides. *Jour. Genetics*, **27**, 91-93.
9. Brocher, F. Observations biologiques sur quelques curculionides aquatiques. *Ann. Biol. Lacustre*, **5**, 180-186.
10. Brues, C. T. Insects as Agents in the Spread of Disease. *Pop. Sci. Mo.*, **81**, 537-550.
11. Brues, C. T. The Possible Etiological Relation of Certain Biting Insects to the Spread of Infantile Paralysis. *Jour. Econ. Entom.*, **5**, 305-324.

12. BUTLER, E. A. Stridulation in British Reduviidae. *Entom. Mo. Mag.*, London, 1912, p. 65.

13. BYRD, H. Bats vs. Mosquitoes. *Canad. Entom.*, **44**, 231-232.

14. CAMPION, F. W. and H. The Feeding Habits of Scorpion-Flies (Panorpidae). *Entom.*, London, 321-322.

15. CASTEEL, D. B. The Behavior of the Honey Bee in Pollen Collecting. *U. S. Dept. Agri., Bureau of Entom.*, Bull. 121, 36 pp.

16. CASTEEL, D. B. The Manipulation of the Wax Scales of the Honey Bee. *U. S. Dept. Agri., Bureau of Entom.*, Circ. 161, 13 pp.

17. COCKERELL. Food Plant of *Dysdercus mimus* Say. *Entom. News*, **23**, 327.

18. COKER, W. C. The Necessity of Water for Flies. *Nature Study Review*, Urbana, Ill., **7**, 277-278.

19. COLLINGE, W. E. On the Locomotion and Length of Life of the Young of *Pulvinaria vitis* var. *ribesiae*. *Jour. Econ. Biol.*, London, **6**, 139-142.

20. COMSTOCK, J. H. The Evolution of the Webs of Spiders. *Ann. Entom. Soc. Amer.*, **5**, 1-10.

21. COMSTOCK, J. H. The Spider Book; A Manual for the Study of Spiders and Their Near Relatives. Doubleday Page and Co., XV + 721 pp.

22. COSENS, A. A Contribution to the Morphology and Biology of Insect Galls. *Trans. Canad. Inst.*, **9**, 297-387, 13 pls.

23. CROFT, E. O. A Notodontid Attacked by a Wasp. *Entom. Mag.*, London, **147**, 13.

24. DOTEN, S. B. Concerning the Relation of Food to Reproductive Activity and Longevity in Certain Hymenopterous Parasites. *Tech. Bull*, No. 78.

25. ESSIG, E. O. Natural Enemies of the Citrus Plant Lice. *Mo. Bull. State Com. Horticulture*, Sacramento, Cal., **1**, 283-296.

26. EWING, H. E. Notes on the Moulting Process of Our Common Red Spider (*Tetrahynchus telarius* L.) (Acarina). *Entom. News*, **23**, 145-148.

27. EWING, H. E. The Origin and Significance of Parasitism in the Acarina. *Trans. Acad. Sci. St. Louis*, **21**, 1-7, pl. I-VII.

28. FABRE, J. H. Die Zirkade und Ihre Feinde. *Zool. Beobachter*, Frankfort a. Main, **53**, 177-184.

28a. FABRE, J. H. Social Life in the Insect World. Translated by BERNARD MIALL. The Century Co., viii + 327 pp.

29. FELT, E. P. Recent Experiments with the Coddling Moth. *Jour. Econ. Entom.*, **5**, 153-169.

30. FERTON, C. Notes détachées sur l'instinct des H. mellifères et ravisseurs, *Ann. Soc. Entom. France*, Paris, **80**, 351-412.

31. GEE, WILSON P. and LATHROP, F. H. Death Feigning in *Conotrachelus nenuphar* Herbst. *Ann. Entom. Soc. Amer.*, **5**, 391-399.

32. GEE, WILSON P. Preliminary List of the Scale Insects of South Carolina with Some Notes on *Lecanium quercifex* Fitch. *Jour. Econ. Entom.*, **5**, 484-486.

33. GIRAULT, A. A. A Few Experiments with the Effects of the Protective Vapors of Heteroptera on Other Insects. *Entom. News*, **23**, 346-352.

34. GIRAULT, A. A. Notes on *Pediculus vestimenti* Nietzsche, the Body Louse of Man. *Entom. News*, **23**, 339-344.

35. GREEN, E. E. On the Occasional Luminosity of the Beetle *Harmatelia bilineata*. *Nature Study Review*, **7**, 212-214.

36. GROSSBECK, S. A. Habits of *Cerceris fumipennis*. *Jour. N. Y. Entom. Soc.*, **20**, 135.

37. GROSSBECK, J. A. Migration of Alabama Argillacea. *Jour. N. Y. Entom. Soc.*, **19**, 259-261.

38. HARVEY, W. Book Scorpions in Captivity. *Country Side*, London, **4**, 432-438.

39. HASENBROCK, K. Ueber die Einwirkung der Roentgenstrahlen auf die Entwicklung der Schmetterlinge. *Inter. Entom. Congr.*, **2**, 195-198.

40. HERMS, W. B. The Reactions of Sarcophid Fly-Larvae to Light. (Abstract). *Jenaische Zeitsch. f. Naturwiss.*, **7**, 152-153.

41. HOFFMAN, F. Zur Biologie der *Cheimatobia brumata*. *Entom. Zeitsch.*, Stuttgart, **25,**, 261.

42. HUNGERFORD, H. B. and WILLIAMS, F. X. Biological Notes on Some Kansas Hymenoptera. *Entom. News.*, **23**, 241-260, pl. XIV-XVI.
43. HUNTER, W. D. Results of Experiments to Determine the Effects of Roentgen Rays upon Insects. *Jour. Econ. Entom.*, **5**, 188-193.
44. JACOBSON, E. Biological Notes on Some Planipennia from Java. *Tydschrift voor Entomologie,* **55**, 97-193.
45. JENNINGS, A. H. Some Problems of Mosquito Control in the Tropics. *Jour. Econ. Entom.*, **5**, 131-142.
46. KEILM, M. Recherches sur les Diptères du Genère Trichocera; Biologie, Développement, Affinities. *Bull. Scientifique de la France et de la Belgique,* Paris, **46**, 172-190.
47. KNAB, FREDERICK. Unconsidered Factors in Disease Transmission by Bloodsucking Insects. *Jour. Econ. Entom.*, **5**, 196-200.
48. KNAB, FREDERICK. The Habits of Flies of the Genus Cordylobia, Parasitic on Man in Africa. *Science*, **35**, 662-663.
49. KORSAKOW, R. Zur geographischen Verbreitung und Biologie der Proturen. *Revue russe d'Entom.*, St. Petersburg, 411-418.
50. LAMBILLION, L. J. L. Quelques remarques biologiques sur la Sésie du Groseillier *(Seisa tipuliformis), Revue Mens. Soc. Entom. Namuroise,* **46**, 62-63.
51. LOUCHEUX, G. La psychologie des bêtes. La mouche verte de la Viande-l'Aslicot. *Le Naturaliste Canadien,* **38**, 165-172.
52. LOVELL, JNO. H. The Origin of the Oligotropic Habit Among Bees. *Entom. News,* **24**, 104-112.
53. LOVELL, JNO. H. The Color Sense of the Honey Bee: The Pollination of Green Flowers. *Amer. Nat.,* **46**, 83-107.
54. McDERMOTT, F. A. The Light Emission of American Lampyridae: Notes and Corrections on Former Papers. *Canad. Entom.*, **44**, 73.
55. McDERMOTT, F. A. Some Further Observations on the Light Emission of the American Lampyridae. The Photogenic Function as a Mating Adaptation in the Photinini. *Canad. Entom.*, **46**, 399-406.
56. MACE, H. The Influence of Weather on Bees. *Nature,* London, **89**, 62-65.
57. MAST, S. O. Behavior of Fire-Flies *(Photinus pyralis)* with Special Reference to the Problem of Orientation. *Jour. Animal Behav.*, **2**, 256-272.
58. MATHESON, ROBT. and CROSBY, C. R. Aquatic Hymenoptera in America. *Ann. Entom. Soc. Amer.*, **5**, 65-71.
59. MAYER, L. Zur Frage der Ueberwinterung von *Pyrameis atlanta. Inter. Entom. Zeitsch.*, **6**, 237-238.
60. MEISSNER, O. Biologische Beobachtungen an *Dixippus morosus*, Nachtrag. *Entom. Zeitsch.*, Stuttgart, **25**, 185-186.
61. MITTERBERGER, K. Zur Biologie *Depressaria pelasitis. Entom. Rundschau,* **29**, 25-27.
62. MOORE, H. W. B. Blood-Sucking Flies Other than Mosquitoes. *Timehri,* **1**, 255-259.
63. MOORE, H. W. B. Ways and Habits of Caterpillars. *Timehri,* **2**, 197-206.
64. MOORE, W. The Tick Problem of South Africa. *Jour. Econ. Entom.*, **5**, 377-384.
65. MORLEY, C. The Cause of " Humming in the Air." *Entom. Mag.,* London, **2** 259-262.
66. NAVAS, P. L. Notes sobre Mirmeleonidos. *Broteria,* **10**, 29-75.
67. OLIVER, E. Les accouplements anormaux chez les Insectes. *Intern. Entom. Congr.,* **2**, 143-144.
68. OMENSETTER, S. The Speech of Insects. *Proc. Del. County Inst. Sci.*, **6**, 121-136.
69. OSBORN, H. A Problem of the Flight of Insects. *Ann. Entom. Soc. Amer.*, **5**, 61-64.
70. PAINE, J. H. The House Fly in Its Relation to City Garbage. *Psyche,* **19**, 156-159.
71. PEARSE, A. S. On the Habits of *Thalassina anomala. Philippine Jour. Sci.*, **6**, 213-215.

72. PETRY, A. Zur Biologie der *Lita vicenella* Frey non Dougl. *Deutsch, Entom. Zeitsch.* " *Iris,*" **26**, 115-118.

73. PIERCE, W. DWIGHT and HOLLOWAY, T. E. Notes on the Biology of *Chelonus texanus* Cres. *Jour. Econ. Entom.*, **5**, 425-428.

74. PORTIER, P. Recherches physiologiques sur les insectes aquatiques. *Arch. Zool. expér. et gén.*, **8**, 89-379.

75. RAU, PHIL and NELLIE. Longevity in Saturnid Moths: an Experimental Study. *Jour. Exper. Zool.*, **12**, 180-204.

76. REGAN, J. Experimentelle Untersuchungen über das Gehör von *Liogryllus campestris. Zool. Anzeig.*, **40**, 305-316.

77. REIFF, W. Ueber den Schmetterlingsfang am Licht. *Inter. Entom. Zeit.*, **6**, 310-311.

78. RICHARDSON, C. H. Notes on the Life History of *Corethra albipes. Psyche*, **19**, 200-203.

79. RILEY, C. F. CURTIS. Observations on the Ecology of Dragon-Fly Nymphs. Reactions to Light and Contact. *Ann. Entom. Soc. Amer.*, **5**, 273-292.

80. RILEY, W. A. Some Remarkable Discoveries Regarding a Common Household Insect. *Ann. Soc. Entom. France*, **35**, 865-866.

81. SAMSONOFF, C. The Activity of *Prospeltella berlesei* against *Diaspis pentagonia* in Italy. (Trans. by. L. O. HOWARD). *Jour. Econ. Entom.*, **6**, 325-328

82. SCHNEIDER, K. C. Orientierung der Bienen. *Natur*, München, **4**, 148-151.

83. SCHOENEMUND, E. Zur Biologie und Morphologie einiger Perla-Arten. *Zool. Jahrbücher*, **34**, 1-56.

84. SEVERIN, H. H. P. and HARTUNG, W. J. The Flight of Two Thousand Marked Male Mediterranean Fruit Flies (*Ceratitis capitata* Wied.). *Ann. Entom. Soc. Amer.*, **5**, 400-407.

85. SHELFORD, VICTOR E. Ecological Succession. IV. Vegetation and the Control of Land Animal Communities. *Biol. Bull.*, **23**, 59-99.

86. SINGH, P. and MAULIK, S. Nature of the Light Emitted by Fireflies. *Nature*, London, **88**, 111. (1911).

87. SLADEN, F. W. L. How Pollen is Collected by the Honey Bee. *Nature*, London, **88**, 586-587.

88. SLADEN, F. W. L. The Humble-Bee, Its Life History and How to Domesticate It; with Description of All the British Species of Bombus and Psithyrus. London, 283 pp.

89. SMIRNOV, D. A. Contribution a l'étude des moeurs et de la metamorphose de *Bruchus affinis* et d'autres Brucides. *Revue russe d'Entom.*, St. Petersburg **11**, 169-194.

90. SNYDER, T. E. Record of Finding a True Queen of *Termes flavipes. Proc. Entom. Soc. Wash.*, **14**, 107-108.

91. STEPHAN, J. Tonerzeugende Raupen und Puppen. *Natur*, München, **3**, 426-427.

92. STEPHAN, J. Tonerzeugende Schmetterlinge, *Natur*, München, **3**, 117-119.

93. STRICKLAND, E. H. A Quiescent Stage in the Development of *Termes flavipes. Jour. N Y. Entom. Soc.*, **19**, 256-259.

94. STUBBS, F. J. The Sense of Fear in Insects. *Zoologist*, London, 158..

95. SZYMANSKI, J. S. Modifications of the Innate Behavior of Cockroaches. *Jour. Animal Behav.*, **2**, 81-90.

96. TOWNSEND, C. H. T. The Possible and Probable Etiology and Transmission of Verruga Fever. *Jour. Econ. Entom.*, **6**, 211-225.

97. TURNER, C. H. An Experimental Investigation of an Apparent Reversal of the Responses to Light of the Roach (*Periplaneta orientalis* L.). *Biol. Bull.*, **23**, 371-386.

98. TURNER, C. H. An Orphan Colony of *Polistes pallipes*, Lepel. *Psyche*, **19**, 184-190.

99. TURNER, C. H. The Copulation of *Ammophila abbreviata, Psyche*, **19**, 137.

100. TURNER, C. H. Reactions of the Mason Wasp, *Trypoxylon albotarsus*, to Light. *Jour. Animal Behav.*, **2**, 353-362.

101. TURNER, C. H. Sphex Overcoming Obstacles. *Psyche*, **19**, 100-102.

102. TURNER, C. H.   Literature for 1911 on the Behavior of Spiders and Insects other than Ants.   *Jour. Animal Behav.*, **2**, 380-399.
103. TURNER, C. H.   Recent Literature on the Behavior of the Higher Invertebrates.   *Psych. Bull.*, **9**, 290-298.
104. WATSON, J. R.   A Foe to the Melon Aphis *Hypodamia convergens* in New Mexico.   *Bull. Univ. New Mexico, Biol. Series*, **3**, 109-119.
105. WEINLAND, H. A.   The Cosmopolitan Habits of the Fruit Fly, *Ceratitis capitata* Weid.   *Pomona College Jour. Entom.*, **4**, 821-825.
106. WEISS, HARRY B.   Notes on *Lixus concavus*.   *Jour. Econ. Entom.*, **5**, 434-436.
107. WINN, A. F.   Notes on the Life History of *Estigmene prima*.   *Canadian Entom.*, **44**, 221-223.
108. WODSEDALEK, J. E.   Formation of Associations in the May-Fly Nymphs *Heptagenia interpunctata* Say.   *Jour. Animal Behav.*, **2**, 1-19.
109. WODSEDALEK, J. E.   Life History and Habits of *Trogoderma tarsale* Melsh., a Museum Pest.   *Ann. Entom. Soc. Amer.*, **5**, 367-381.
110. WODSEDALEK, J. E.   Natural History and General Behavior of the Ephemeridae Nymphs *Heptagenia interpunctata* Say.   *Ann. Entom. Soc. Amer.*, **5**, 31-40.

LITERATURE FOR 1912 ON THE BEHAVIOR OF ANTS AND MYRMECOPHILES

WILLIAM M. MANN

Bussey Institution, Harvard University

Miss Andries (1) made a detailed study of the taxonomy, biology and development of the German species of flies of the genus Microdon, which in their larval and pupal stages live in ant nests. The species studied (*M. rhenanus, mutabilis* and *eggeri*) live most commonly with species of Formica, though the forms of *eggeri* were found also with Lasius. Fertilized females of the fly readily oviposited on bark, inserting the ovipositor into cracks. About one hundred and fifty eggs are laid, five to eighteen in a lot. These hatch in about twelve days. The larvae are not unlike certain slugs, and in fact were described by some early writers as mollusks. They crawl slowly about in the nest, secreting from the mouth a fluid that keeps the under side of the body moist. The food habits are not understood. Andries thinks that they feed on the vegetable moisture in the nest, as no solid food was found in any of the specimens sectioned. The relationship of the fly in its different stages to the ants is not well understood. It was formerly supposed by Wasmann that the larvae were treated like big Coccidae. Those kept by Andries were entirely ignored by the ants, and it was noted that when nests in the field were disturbed the ants removed their brood to a place of safety, while the Microdon larvae remained behind unnoticed. Wasmann has observed the ants lick the golden hairs of freshly emerged adults, but Andries notes that the adults, both in the field and in observation nests, were treated inimically by the ants, which seized them by the legs and wings. She succeeded in bringing growing larvae through to the adult stage apart from ants, and does not believe that Microdon is closely dependent upon its host.

Brun (3), after numerous experiments on the colony forming habits of Formica, believes that the higher acervicolous species in the genus are descended not only morphologically, but also

biologically, from the *fusca* group, that is, from a *fusca*-like ancestor. In *fusca*, the habit of two or more queens jointly forming a colony—"pleometrosis" of Wasmann—sometimes occurs, but with this ant it is merely an occasional method of colony-formation. The typical method, according to which the individual female after the marriage flight starts her colony unaided, is most general. In *F. pratensis* and *F. rufa* pleometrosis is more fully developed, and is of use in splitting up the colony into branches, and by means of these extending the colony in the near vicinity. Brun considers that the great success of *rufa* as a species is accounted for by this habit of colony splitting. The origin of this branch-forming habit has been explained by Wasmann as an adaptation to special methods of life. *Rufa* and *pratensis* have become adapted to life in certain ecological situations, in which they are sporadically very abundant, in contrast to other more widely adaptable ants such as Lasius, Tetramorium, etc., which occur in nearly all kinds of localities. The special vegetative conditions to which *rufa* and *pratensis* are adapted are exhausted after the long residence of an ant colony in one place, and then it is beneficial to be able to split the colony, and enable it to spread in the immediate vicinity where the conditions are the same, rather than to send off swarms to less favorable localities. This branching can be accomplished by the raising of reserve queens, which produce branch nests for the excess workers. Each season, during the time of flight, large numbers of sexual forms are held back in the nest. This habit has gradually modified the normal instinct of the female, the mneme of which has thus been weakened ("büszt an Frische ein"). After the marriage flight the normal instinct of an ant queen is to dig a hidden chamber, but in *rufa*, whose ancestors were continually surrounded by workers, because of the inherited engrammes, there is developed a strong "social desire," which drives it to seek worker society. Here there are three possibilities. The female may return to one of the peripheral nests of the mother colony, becoming in reality parasitic on the members of her own colony, which is the first stage in social parasitism. Many do not reach their own colonies, but find other nests of the same species, or of another race and take up with them, while a comparatively small number, reaching *rufa*-free ground, enter the nests of strange species. This latter is the

last stage of social parasitism. It is thus shown that the social parasitism of *rufa* is derived from pleometrosis through a number of steps. That all of these intermediate stages occur in this species shows that *rufa* must still stand in a primitive condition as far as social parasitism is concerned. Wheeler has had a tendency to consider *rufa* as an obligatory social parasite (both Brun and Wasmann evidently fail to understand his position in regard to this matter), but Brun agrees with the theory of Wasmann, and furthermore endeavors to strengthen this view by an appeal to the engramme-theory of Semon, that pleometrosis necessarily causes degeneration and final loss of the colony-forming instinct, thereby giving a psychological foundation to the theory. From the standpoint also of paleontology, morphology and geographical distribution Wasmann's theory seems to be correct. Brun agrees with Wasmann also in considering that *F. sanguinea* approaches the *rufa* type biologically, and therefore has been derived from a *rufa*-like form. Emery, Viehmeyer and Wheeler, who have opposed Wasmann's theory and to some degree upset it, have maintained that, "A robber cannot be derived from a parasite," hence a robber ant, during its development, can never traverse the stage of social parasitism, even as a facultative one, as in *rufa*. They all look upon the pupal robbing habit as a distinctive mode of colony formation from which dulosis is supposed to have developed on one hand and social parasitism on the other, thus accepting the robber-female theory of Emery. As Wasmann himself has answered many of the attacks on his theory, Brun does not undertake to go into all of the criticism, but defends Wasmann on the ground that Viehmeyer must have misunderstood him. Wasmann never contended that the predatory stage of *sanguinea* is derived from a parasitic stage. The *sanguinea* group does not go back to *rufa*, but comes from a *rufa*-like form, which had a tendency toward pleometrosis and branch-colony formation, and thereby lost its ability to form independent colonies. From such ancestors there branched off a particularly viable race with high psycho-plastic tendencies, part of whose females, after the ancient manner, allow themselves to be taken up by the same species; others, "having higher attainments," since they could not accomplish this, took to robbing pupae, or made up to a colony founding *fusca* queen, which they later robbed or mur-

dered.   Regarded in this way, the familiar statement that parasites cannot become robbers loses its significance as an argument
against the derivation of *sanguinea* from *rufa*-like ancestors, for
sanguinea comes not from *rufa*, but from a *rufa*-like type, with
a loss of colony-foundation instincts, which does not involve
parasitism.   Neither does this mean degeneration, but rather a
high development, as in the present day *rufa*.   Viehmeyer's
opinion that these species are doomed to extinction seems
"curious" to Brun, considering the immense size of the colonies of *rufa;* as "curious" as the organic and psychical degeneration which he thinks he finds in the high psycho-plastic endowment of *sanguinea*.   In saving the psycho-phylogeny of his
robber stages, Viehmeyer assumes that the females of *sanguinea*
originally took part in the robber raids of their colonies, but
this opinion is too uncertain to be taken seriously in the discussion.   Brun concedes Wasmann's derivation of dulosis in
Formica from a facultative adaption stage to be the weakest
part of his theory.   The apparent analogy of permanent dulosis
and temporary parasitic colony foundation will not stand strong
criticism, because we do not know that the colonies are exclusively founded with the aid of *fusca*.   We can account for the
social parasitic condition of *rufa* only by assuming a condition
involving the loss of the ability to establish a colony unaided,
and this loss could have been due as directly to the pupal-
robbing habit as to obligatory social parasitism.   Wasmann did
not mean that a subparasitic condition was a step toward dulosis, any more than he wished to deduce the already developed
social parasitism from dulosis.   He considers dulosis in *sanguinea*
a direct engraphic influence.   Through the presence of *fusca* in
the nest the young *sanguineas* are influenced to raise the *fusca*
pupæ obtained by raids, and care only for those whose smell is
similar to their own.   This psychological reason of Wasmann
does not seem to Brun to hold, for the tendency of *sanguinea*
is not limited to *fusca* pupae, but extends also to allied species.
This, Brun explains, is a fixed, inherited association from analogy.   The workers in colonies not socially parasitic often show
just as strong a tendency toward dulosis.

    Brun is not inclined towards Wasmann's hypothesis of the
origin of dulosis in *Formica* from facultative social parasitism,

but does lean toward his theory that the social parasitic stages were derived from a *rufa*-like form.

Brun (3) believes that the theory of the mixture of odors, which has been used to explain, in a purely physiological way, the tolerance of one species toward another in the artificial alliances of certain species of ants, must be given up, as entirely untenable. These artificial alliances do not depend upon the mixture of odor, but depend entirely upon complex associative brain processes, especially in the realm of individually acquired mnemic engrammes.

Cornetz (5) believes that the apparent coöperation of several ants in moving particles of food too large to be handled by a single individual is simply the result of the stimulus that causes the solitary ant to return home. When an ant starts on a foraging trip it receives, in some manner, an impression that later guides it back to the nest. When it finds a morsel of food it takes it, and returns by an almost direct route. Several ants, having hold of a morsel too large for a single one, are each guided by this direction-sense toward the nest, with the result that the combined efforts of many holding and pulling the piece of food are used to bear it. This gives at first sight the impression of mutual aid, but is in reality only "a fortuitous coincidence of purely individual actions." There is even actual hindrance to one another when many have hold of the same morsel. Likewise, other actions at first sight mutualistic are believed to be simply the result of individual activity or of a certain tendency toward imitation, comparable to the flocking of sheep. Thus, Cornetz saw an isolated worker digging at a new nest some distance away from the principal nest. In another instance seven workers were engaged in working at a gallery far from the nest. These carried eggs, larvae and even adults from the original formicary, in which, however, most of the colony remained. This division was in no sense beneficial to the entire community, but was probably the result of several workers following one that had started the new gallery. As the worker is merely an undeveloped female, the tendency to establish a new colony is not surprising, as often other female characters are more or less developed in individual workers, even parthogenetic reproduction, and the nest-forming habit is typically female. When one worker begins to dig a new nest, others coöperate

through imitation. Cornetz does not believe that the social coöperation of ants is altogether a result of individual action, but points out that there may be much less mutualism than is generally believed.

Cornetz (8) believes from a study of Myrmecocystus that this ant has, to a greater or less extent, an impression of the territory immediately surrounding the nest entrance, but that this memory is inconstant and of short duration, especially when based upon the visual sense. When the memory is olfactive it may persist for a long time.

Cornetz (10) compares the sense of direction of the rat and the ant. The rat observed by Szymanski (Essais pour exprimer par des nombres le rapport entre des stimulants de genres differents. *Archiv. f. d. ges. Physiol.*, Bonn, 1912) when liberated in a box containing a pan of water wandered about until it found this, but each succeeding time, by the "dropping of useless movements," shortened the distance traveled, till it finally went directly to the water. On each trip the rat had revived impressions that had been received on the previous trips. The ant, on the other hand, is guided by an impression received on each outgoing journey, and revived on the homegoing route. To what extent the ant is able to remember a direction "to the right" or "to the left" is still completely unknown, but Cornetz ventures the hypothesis that the ant does not need a memory, but possesses "en soi" a sense of direction. This he believes to be not at all impossible, though hard to conceive.

Cornetz (10a) experimented on the estimation of distance in ants. Workers of *Pheidole pallidula* away from the nest were decoyed by little pieces of cheese on to a knife blade, and taken to a point at a short distance away. When the ant dismounted from the blade it set out in a line parallel and opposite to the outgoing trail, reversing the direction of march in the manner usual to ants, but owing to the change of the starting point, not in the direction of the nest. Cornetz made careful comparison of the distance traveled on the wrong trail, and the distance to the nest if the ant had not been moved to another starting point. Where both trails were on the same kind of material, there was an error of from one-tenth to one-fifth of the distance, though one ant erred by three-fifths, which is an abnormal amount. When the trails were different (one on cement and the other on

bricks) the error ranged from one-sixth to nine-tenths of the distance. On a longer journey the error was still greater. The start in a direction the reverse of the line of march in the outward journey, even when not toward the nest, and on different kinds of material, offers additional evidence that the home-going ant is influenced little by sight or the sense of touch.

Cornetz (7) repeated the experiment of turning a disc on which an ant (*Myrmecocystus* (*Cataglyphis*) *bicolor*) was feeding. The disc in this case was a large plate, containing sugar as bait. Each time the ant, when it was through feeding and had a load of the food, immediately oriented itself in the direction toward its nest-entrance, though the disc had been turned 180 or 270°. The podometric sense, according to Cornetz, will not explain the return of the ant, both because "a podometer is no compass" and because the route taken by the returning insect is not the same as the outgoing trip. He answers the question, "How do ants find their way," by stating that they do not find their way. It is not necessary. They are guided by some internal impression received on the outgoing trip. Just what this is, he does not pretend to understand, but he believe that it is neither touch, smell nor sight, nor a combination of these, but something peculiar, possessed by all ants.

Crawley (11) studied parthenogenetic reproduction in *Lasius niger*, with colonies confined in artificial nests. It has long been known that under certain conditions, generally when no queen is present, worker ants are capable of laying unfertilized eggs that develop parthenogenetically. Some observers have concluded that only males are produced from these worker-laid eggs, but in 1902 a queenless colony of *Lasius niger*, kept under observation by Reichenbach, reared some three hundred workers and two or three dozen males from unfertilized eggs, and Wheeler in 1903 recorded similar results obtained by Mrs. Comstock with *Lasius niger* var. *americanus*. On the other hand, Janet, who made careful experiments with no less than thirty queenless colonies under varied conditions, succeeded only in getting males. Into a nest of *Lasius niger* that had lost its queen through accident, Crawley placed a queen of *Lasius umbratus* which was immediately adopted. Although this queen deposited many fertile eggs, for two years none of the young reached maturity, as they were eaten by the *niger* workers; thereafter the few

that did mature were immediately killed and eaten, or fed to the other larvae. During this time several hundred *niger* workers reached maturity. In another similarly composed colony the results were the same. During four years no males were produced. A third nest again containing a queen of *L. umbratus* and *niger* workers, with no brood at the start, produced only *niger* workers, normal in all respects except that they were somewhat undersized. Twelve workers were carefully dissected in order to ascertain if a receptaculum seminis was present. This was not found, so the experiment confirms that of Reichenbach and shows that in parthogenetic reproduction by worker ants, workers as well as males may result.

Crawley (12) found in England a colony of the parasitic ant *Anergates atratulus* in a *Tetramorium caespitum* nest. No sexual forms of the latter species were present. The male Anergates is wingless, and copulation takes place in the nest. The queens kept by Crawley removed their wings shortly after copulation, and made no attempt to leave the colony, but each queen seized a Tetramorium worker by the antennae and kept hold of it for hours. This habit may be useful in getting the queen into a strange nest, and may have for its object the acquisition of the odor of the Tetramorium. A colony of the latter ant that had adopted a newly fertilized Anergates queen, killed off all the sexual forms of its own species in the nest, including two dealated queens.

Donisthorpe (13) found colonies of *Leptothorax acervorum* and *Myrmica laevinodis* beneath the same stone. When the nest was disturbed they showed no antagonism toward each other, and if they picked up each other's larvae or pupae they put them down again. Small larvae of the fly *Microdon mutabilis* kept in an artificial nest with *Formica fusca* grew to a large size without being fed by the ants or feeding on the honey provided for them. When the ants moved, the Microdon followed them very slowly. It is evident that they feed on the droppings and pellets rejected from the buccal chamber of the ants. *Antennophorus uhlmanni*, which lives attached to *Lasius umbratus*, was observed to move to one side of the ant's head in order to permit it to feed.

Donisthorpe and Crawley (14) made a number of experiments on the founding of colonies by queens of *Lasius fuliginosus*. It

had long been supposed that this species was a temporary social parasite of *Lasius umbratus* and its varieties. A queen of the former species placed in *umbratus* colonies was not attacked at once, as is generally the case when a queen ant is introduced into a strange colony, but in some instances was attacked later on. When some part of her body was being held by an inimical worker, she endeavored to conciliate it by caressing with her antennae, and often succeeded. Some of the queens on which experiments were made were persistently molested and finally killed, but several were fully adopted and had larvae and pupae at the time the record of the experiment stopped. This shows that *fuliginosus* is a temporary social parasite of *umbratus*, which itself is parasitic in turn on *L. niger*. Several pupae of *niger* were placed in a nest of *umbratus*, in order to ascertain if the latter had any friendly instincts remaining toward the species in a colony of which it had begun its existence. The pupae were carried about; but were left too long before being opened so that most of the ants that emerged were crippled. These were bullied by the *umbratus*, but two perfectly healthy individuals were living in the nest, unmolested, at the time of writing.

Emery (15) observed that the eggs laid by workers of a harvesting ant, *Messor barbarus minor*, produced only males. The larvae were different in appearance from those which produced females and workers, so he concludes that sexual dimorphism is apparent also during larval stages. The same species was offered oats which had germinated and from which the husks had been removed. These were chewed by the ants till they became a ductile mass, from which the nutritive portions had been extracted. Dried oats, not germinated, were put in the nest. The ants ate first the embryo and the end of the grain where this was located, a habit that had been noticed by the ancients and which was mentioned by Plutarch. When the embryos and the farinaceous parts of the seed were separated and each ground up and made into a paste by the addition of water, the ants showed a decided preference for the paste made from the embryonic portion, especially when it was the more humid of the two. The cutting of the radicles of the seed by grain-storing ants may be the result of this fondness for the germinal portion. Italian paste in small ring-shaped pieces

which had been carefully weighed was placed before the ants
in their nest, and the discarded refuse and pellets were after-
wards weighed and a chemical analysis of the substance was
made both before and after the ants had had access to it, so as
to ascertain just what proportion of the total quantity and
what nutritive properties of each had been consumed. Some
of the paste was fed by the ants to their larvae after being
softened by malaxation. The larvae ate this readily, so Emery
decided that the making of "larval bread" as described by
Neger, is not necessary. The workers consumed about 7.3% of
the starch in the paste in order to digest it or give it as food to
the larvae. The quantity of non-starchy foods was not ascer-
tained, but Emery assumes that the nitrogenous portions are
more important than starch.

The harvesting ants are descended from insectivorous forms,
which have taken up the grain-storing habit as an adaptation
to life in the desert, on steppes, etc., where during parts of the
year insect food is scarce. Seeds can be stored and kept, which
is not true of insect food. Emery notes that the species studied,
though a typical harvesting ant, never refuses insect food.

Ernst (16) placed a number of queens of *Lasius flavus* in an
artificial nest. Eggs laid by these developed rather slowly, but
produced larvae and imagines. The latter, while yet callows,
disappeared, and Ernst found portions of their bodies and in
the same place two individuals of the mite, *Laelaps oöphilus*,
which must have been introduced into the nest on the bodies
of the females. The number of mites increased very rapidly
till the bottom, sides and covers of the nest, twelve by nine cm.
in dimensions, were swarming with them. Many were among
the eggs and even crawled upon the ants' heads, from which
they were dislodged by vigorous shaking. A living callow lying
on the bottom of the nest was seen to be attacked by numerous
mites, most of which were on the thorax and legs. The next
morning only portions of the ant were found, the probability
being that the mites had taken it to pieces, though this was not
actually seen. The mites in the nest died off very suddenly, so
observations could not be continued. Ernst, from a long series
of observations, believes that ants are capable of forming attach-
ments to one another. Though an ant recognizes and is friendly

to others of the same colony it does not generally associate with one particular individual more than with others, but Ernst observed that two isolated ants showed an attraction for each other, remaining together much of the time, and when one died the other showed signs of much uneasiness. In the case of two females and a worker of *Tapinoma erraticum* which were kept isolated, the former seemed much disturbed at the death of the latter, licking and feeling of the body. These actions were more pronounced in one of the females than in the other. A female of *Formica rufibarbis*, after killing two females of *F. pratensis*, received a third without signs of hostility, and the two lived amicably together. Different species of ants vary in their aptitude for making friends, and the females form the association more quickly than the males. Ernst observed a Dipteron, *Farnia manicata*, in company with ants, in the act of "milking" aphids and sipping up the drop of exuded liquid. The fly stroked the gaster of the aphid with its forefeet, which are provided with a brush of hairs.

Besides ants and this interesting dipteron, a Lycaenid butterfly in Ceylon is known to milk aphids.

Hungerford and Williams (17) in Kansas observed that the great majority of nests of *Pogonomyrmex occidentalis* have their openings on the southeast side or more toward the east. A heliotropic influence is suggested.

A special disgust was shown by the workers toward certain Scaraboeid beetles. When one of these was placed on the nest it was attacked by as many as ten workers, and when it had ceased struggling was carried to a distance of ten or twelve feet from the cone. The ant was seen carrying the myrmecophilous beetle *Cremastocheilus saucius*.

Hunter (18) notes that in fields infested with the agricultural ant, *Pogonomyrmex barbatus* var. *molefaciens*, the plants in a circle just outside the cleared areas of the nest grow with increased luxuriance, a condition he thinks, caused by the loosening of the soil through the underground tunnels of the ants, which has somewhat the effect of deep plowing. This increased growth is, in a way, compensatory for the cleared areas which the ants make, and though it does not entirely offset the loss caused by them, reduces the economic importance of the insect.

The actual damage caused by these ants is said by Mr. J. D. Mitchell, who has made many observations on the species, to be greatly overestimated.

Von Ihering (19) in Brazil found nests of the army ant, *Eciton coecum*, deep in the earth beneath termite nests. It has long been supposed that ants of the genus Eciton do not make permanent nests, but move about from place to place. At times clusters have been found with many workers, larvae and pupae, and often a female, and these have been considered temporary nests. Von Ihering thinks that these are swarms. The female, blind and wingless, is not capable of founding a colony unaided, after the manner of most queen ants, and new colonies are established by means of a "swarm," composed of a queen and numerous workers, often accompanied by males. Sometimes males of different species are present, and von Ihering thinks that hybridization may not be uncommon among the species of Eciton.

Jacobson (20) in Java observed the larvae of the butterfly, *Hypolycaena erylus*, which is attended by the ant *Oecophylla smaragdina*. Both of these insects were common on the rubiaceous plant *Banguersia spinosa*. The butterfly lays her eggs on a plant tenanted by the ants. These attend the larva, and by caressing it receive a drop of exuded liquid which is eagerly lapped up. A considerable amount of this liquid is secreted by a single larva during the course of a day. Larvae under observation, not attended by ants, became listless and later died, so there is evidently a close though not well understood, symbiotic relation between the two insects. The pupae also were cared for and licked, though in them there is no evident food supply for the ants.

Lea (21) in a supplement to a paper on the Australian and Tasmanian Coleoptera inhabiting or resorting to the nests of ants, bees and termites (Proc. Roy. Soc. Victoria, Vol. XXIII, (New Series, pt. 1, 1910.)) lists and describes a large number of myrmecophilous and termitophilous beetles. Through the energies of Mr. Lea and his co-workers the very rich ant-nest fauna of Australia and Tasmania is becoming comparatively well known. It is an interesting fact that the ponerine ants of those islands, especially *Ectatoma metallicum*, harbor a preponderant number of the inquilines.

Leonard (22) observed workers of *Messor andrei* after a heavy rain carrying out members of the colony which were covered with mud and quite lethargic. After these had remained in the warm sunshine for a time they returned into the nest. Leonard assumes that they had suffered from the wetting and the nest-mates had carried them out where they might revive.

Lucas (23) notes that in a colony composed of about twenty workers, without a queen, of *Formica fusca* in an artificial nest, eggs were deposited parthogenetically. These were either eaten or neglected by the ants, so none developed.

Malloch (25) in a monographic revision of the dipterous family Phoridae lists sixteen North American species that are known to be associated with ants. Most of these are parasitic, though one species, *Metopina pachycondylae*, is known to live as a commensal with *Pachycondyla harpax* in Texas.

Mann (26) observed the Proctutrypid *Mimopria ecitono-phila*, with *Eciton hamatum*, the host ant. The parasite runs along with the army of workers in an ant-like manner, and is sometimes picked up and carried by the ecitons.

Mann (27) found in Brazil a Ponerine ant, *Odontomachus affinus* subsp. *mayi*, living in company with *Dolichoderus debilis* var. *rufescens*, in an arboreal earthy nest constructed by the latter species. Odontomachus generally nests in damp places such as beneath stones or logs. In the earthy nest of Dolichoderus this variety finds a suitable arboreal environment, and being a powerful, stinging ant, is very probably useful to the Dolichoderus in defending the nest.

Newcomer (28) in California studied the caterpillars of *Lycaena fulla* and *L. pseudargiolus* var. *piasus* in their relation to ants. The latter species in the third and fourth instars is very generally attended by *Tapinoma sessile* and *Prenolepis imparis* and occasionally by Crematogaster and Camponotus. An ant, on discovering a larva, proceeds to stroke its posterior segments with the antennae, and to feel about with its palpi. If the ant touches the evaginable organs of the eleventh segment it immediately becomes greatly excited and runs about as though irritated. The sharp projections on the setae of these organs evidently irritate the sensitive antennae, and thus act as a repellant when the caterpillar is not able to exude the liquid which the ant desires. A caterpillar may be disturbed several

times by the ant before the slit on the tenth segment opens and the papilla which bears the drop of liquid is thrust out. The ant laps this up, while it is stroking the larva with its antennae. *L. piasus* emits a drop of the liquid about once every fifteen minutes. The stroking of the larva by the ants acts as a stimulus which causes either the ejection of the liquid or, in case the organs are not in a condition to exude, the eversion of the repellant organs of the eleventh segment.

Piéron (29) gives a general survey of the observations and experiments by various investigators on the problem of orientation in ants. As far back as 1745, when Bonnet published on the subject, it has been known that the sense of smell plays an important rôle in guiding the ant back to its nest. Huber, Forel, Bethe and others have confirmed this, till there is no doubt as to its truth, and Santschi has recently shown that certain species by means of touching the ground with the tip of the gaster actually make an odoriferous "intentional" trail. The differences in this trail, which naturally varies in intensity close to and remote from the nest, are appreciated by the "topochemic sense" (Forel) and are therefore valuable in orienting the home-going ant. Odor plays a more important rôle with those ants which have a collective trail, except in some forms, like the wandering Ecitons and the slave-making Polyergus, the armies of which do not return directly by the outgoing trail. In the case of isolated foraging ants, in the environs of the nest, it is probable that sight, smell and touch are all employed, different forms of ants varying in the degree in which these various senses are used. Thus Lasius is considered by Piéron to be an olfactive type, Formica and Camponotus visual types and Messor a muscular type. Orientation at a distance from the nest opening has been explained in a number of ways, and it is probable that the muscular memory and the influence of the light are both important elements, though neither fully explains the problem. The ant does not exactly retrace its steps and probably makes more movements on the out-going than on the returning trip, which may cause considerable error in locating the nest again, while the impression given by the light is obviously received only by diurnal species. Piéron points out that the agricultural ants—Messor—of Erytrea stop

foraging at the close of the day, and asks if this could be caused by the need of the direct influence of the light for guidance.

In addition to light and the muscular memory there must be some other influence. Two hypotheses are suggested. Either the ant possesses a magnetic sense, or there is some internal organ that records sensations made in describing angles on the out-going trail.

Ruschkamp (31) found in Holland the first stage of an adoption-colony of *Formica rufa* by *F. fusca*. A single deälated *rufa* queen was in a nest occupied by a weak *fusca* colony. No *fusca* queen was present. This mixed colony was placed in an artificial nest and observed for some time. The alien queen had been completely adopted.

Wasmann (32) describes an extraordinary Staphylinid beetle, found in West Africa with the army ant, *Dorylus (Annoma) nigricans* subsp. *sjostedti*. This beetle, named *Mimanomma spectrum*, is a most striking example of mimicry, with greatly elongated thorax, short, thick antennae and ant-like abdomen. The latter has the first two segments small and constricted, resembling in form the petiole and post-petiole of Annoma, and the general form of the body is more ant-like than even the Staphylinid *Mimeciton pulex*, hitherto the most remarkable ant mimic among the beetles. A number of species of the family Staphylinidae are exceedingly similar in form to the ants with which they live; also some of the parasitic Hymenoptera and even Diptera which live with ants resemble them closely, but none are so greatly modified as this new species described by Wasmann.

Wasmann (33) gives a list of some forty species of inquilines recorded from the nests of one species of ant, *Solenopsis geminata*. These represent the orders Coleoptera, Diptera, Hymenoptera, Thysanura, Acarinae and Diplopoda. A number of guests of East Indian species of Pheidole are listed also, and several new species of myrmecophilous Coleoptera are described.

Wasmann considers that the adaptations to myrmecophily in the European lady-beetle, *Coccinella distincta*, present a Darwinian paradox. The larva of this beetle lives unmolested in the nests of species of Camponotus and Formica, where it feeds on scale insects which are fostered by the ants and from which

the ants receive part of their food supply, and is therefore inimical to the welfare of the ant community. Such an association, Wasmann thinks, could not have been brought about by natural selection. That selection is a factor in evolution is admitted, but it does not play a leading rôle.

Wheeler (34) describes a peculiar coenobiotic association which he found in Arizona. Five or six organisms coöperate to form this. The oak, common in the Huachuca Mountains, was heavily infested with the mistletoe. Larvae of a weevil had made their borings in this, and these were tenanted by colonies of the ant *Cremastogaster arizonensis.* On the inside of the ant galleries were numerous scale insects, later described by Cockerell as *Pseudococcus phoradnedri,* which slowly kill the mistletoe. Thus the ant, which fosters scales injurious to the mistletoe which is a serious parasite of the live oaks and other trees, may be regarded as a useful forest insect.

Zimmer (35) records the finding of a nest of *Lasius fuliginosus* in a child's coffin which had been buried for about thirty years. The entire interior of the coffin was filled with carton made by the ants.

REFERENCES

1. ANDRIES, MARIA. Zur Systematik, Biologie und Entwicklung von Microdon Meigen. *Zeit. f. wiss. Zool.,* **103,** 300-361.
2. BRUN, EDGAR. Ueber die Ursachen der kunstlichen Allianzen bei den Ameisen, ein Problem der vergleichenden Psychologie. *Zeit. f. wiss. Insektenbiol.,* **8,** 334-.
3. BRUN, RUDOLF. Zur Psychologie der kunstlichen Allianzkolonien bei den Ameisen. *Biol. Cent.,* **32,** 308-322.
4. BRUN, RUDOLF. Weitere Beiträge zur Frage der Koloniegrundung bei den Ameisen, mit besonderer Berücksichtigung der Phylogenese des sozialen Parasitimus und der Dulosis bei Formica. *Biol. Cent.,* **32,** 154-180, 216-226.
5. CORNETZ, V. L'illusion de l'entraide chez la fourmi. *Rev. des Idées,* 15 Dec. 1912, 1-12.
6. CORNETZ, VICTOR. Ueber den Gebrauch des Ausdruckes "tropische" und über den Charakter der Richtungskraft bei Ameisen. *Arch. f. d. ges. Physiol.,* **147,** 215-233.
7. CORNETZ, V. Observations de fourmis recruteueses de l'espèce *Myrmecocystus cataglyphis bicolor. Bull. Inst. gén. Psych.,* **12,** 79-90.
8. CORNETZ, V. De la durée de la mémoire des lieux chez la fourmi. *Arch. de Psychol.,* **12,** 122-138.
9. CORNETZ, V. Les fourmis voient-elles des radiations solaires traversant les corps opaques. *Bull. Inst. gén. psych.,* **12,** 367-372.
10. CORNETZ, V. Comparison entre la prise d'une direction chez un rat et chez une fourmi. *Bull. Inst. gén. Psych.,* **12,** 357-366.
10a. CORNETZ, V. Quelques observations sur l'estimation de la distance chez la fourmi. *Bull. Soc. Hist. Nat. de l'Afrique du Nord. Jan.,* 1912.
11. CRAWLEY, W. C. Parthenogenesis in Worker Ants, with special réference to two colonies of *Lasius niger,* Linn. *Trans. Ent Soc. London,* Feb. 10, 1912, 657-663.

12. CRAWLEY, W. C. *Anergates atratulus* Schenk., a British Ant, and the Accept-
ance of a female by *Tetramorium caespitum*, L. *Ent. Record, Jour. Var.*,
24, 218-219.
13. DONISTHORPE, H. ST. J. K. Myrmecophilous Notes for 1911. *Ent. Record*,
24, 4-10, 34-40.
14. DONISTHORPE, ST. J. K. and CRAWLEY, W. C. Experiments on the Formation
of Colonies by *Lasius fuliginosus*. *Trans. Ent. Soc. London*, Feb. 10, 1912.
664-672.
15. EMERY, CARLO. Alcune esperienze sulle Formiche granivore. *Rend. Sess. R.
Acad. Sci. Ist. Bologna*, 1912, pp. 107-117.
16. ERNST, CHRISTIAN. Neue Beobachtungen bei Ameisen. *Biol. Cent.*, **32,** 146-
153.
17. HUNGERFORD, H. B., and FRANCIS X. WILLIAMS. Biological Notes on some
Kansas Hymenoptera. *Ent. News*, **23,** 241-260.
18. HUNTER, W. D. Two Destructive Texas Ants. *U. S. Dept. Agric. Circ. No.
148.* 1-7.
19. VON IHERING, H. Biologie und Verbreitung der brasilianischen Arten von
Eciton. *Ent. Mittheil.*, I, No. 8, pp. 226-235.
20. JACOBSON, EDW. Symbiose zwischen der Raupe von *Hypolycaena erylus* Godart
und *Oecophylla smaragdina* Fab. *Tijdschr. fur Entom.*, **55,** 9-14.
21. LEA, A. M. Australian and Tasmanian Coleoptera Inhabiting or Resorting to
the Nests of Ants, Bees and Termites. *Supplement. Proc. Roy. Soc. Victoria*,
25, (New Series), Pt. 1, 31-78.
22. LEONARD, PERCY. The Emmet Harvesters of Point Loma. *The Theosophical
Path.*, **2,** No. 3, March, 1912, 215-216.
23. LUCAS, KARL. Parthenogenese bei der grauschwarzen Waldameise (*Formica
fusca* L.). *Zeitschr. f. wiss. Insektenbiol.*, **8,** 272-276.
24. LUJA, EDOUARD. Moeurs des Anomma. *Monatsber. Ges. Luxemburg. Natur-
freunde,* N. F. Jahrg. 3, 94-97.
25. MALLOCH, J. R. The Dipterous Insects of the Family Phoridae in the United
States National Museum. *Proc. U. S. Nat. Mus.*, **43,** 411-529.
26. MANN, WILLIAM M. The Stanford Expedition to Brazil, 1911. J. C. BRANNER,
Director. Note on a Guest of *Eciton hamatum* Fabr. *Psyche*, **19,** 98-100.
27. MANN, WILLIAM M. The Stanford Expedition to Brazil, 1911. J. C. BRANNER,
Director. Parabiosis in Brazilian Ants. (Contrib. Entom. Lab. Bussey Inst.
Harvard Univ. No. 54). *Psyche*, **19,** 36-41.
28. NEWCOMER, E. J. Some Observations on the Relations of Ants and Lycaenid
Caterpillars, and a Description of the Relational Organs of the Latter. *Jour.
N. Y. Entom. Soc.*, **20,** 31-36.
29. PIÉRON, H. Le problème de l'orientation envisagé chez les fourmis. *Scientia*,
12, 217-243.
30. PLAUT, MENKO. Ueber die Symbiose bei Ameisenpflanzen. Neuere Arbeiten
zur Kritik der Theorie Schimpers. *Monatsh. nat. Unterr.*, **5,** 33-37.
31. RUSCHKAMP, F. Eine neue natürliche *rufa-fusca* Adoptionskolonie. *Biol.
Cent.*, **32,** 213-216.
32. WASMANN, E. *Mimanomma spectrum*, ein neuer Dorylinengast des extremsten
Mimikrytypus. *Zool. Anzeig.*, **39,** 473-481.
33. WASMANN, E. Neue Beiträge zur Kenntnis der Termitophilen und Myrmeco-
philen (No. 192). *Zeit. f. wiss. Zool.*, **101,** 70-115.
34. WHEELER, WILLIAM MORTON. Notes on a Mistletoe Ant. *Jour. N. Y. Entom.
Soc.*, **20,** 130-134.
35. ZIMMER, C. Nest von *Lasius fuliginosus* Latr. in einem Sarge. *Zeit. f. wiss
Insektenbiol.*, **8,** Heft 1, 32.

LITERATURE FOR 1912 ON THE BEHAVIOR OF VERTEBRATES

JOHN B. WATSON AND K. S. LASHLEY*

VISION

Fish. Loeb (16) discusses briefly the problem of color and pattern adaptation in the flat-fish. He is inclined to accept the suggestion of Munk and Henschen that in vision there is formed an image, not only upon the retina, but also upon the cortex, and to develop such a view even farther. Taking as a foundation the work of Sumner in which it was shown that the flounder was able to reproduce rather complicated patterns upon its skin, Loeb assumes a point for point correspondence between the retinal image and the pattern formed upon the skin. The mechanism of this process is expressed in two sentences:—"Es liegt nahe, anzunehmen, dass jeder Punkt des Retinabildes ein Reizpunkt ist, welcher einen entsprechenden Bildpunkt durch Vermittlung einer Nervenfaser in den primären Optikusganglien hervorruft. Jeder Bildpunkt in den primären Optikusganglien kann wieder als Reizpunkt angesehen werden, der durch Vermittlung einer besonderen Nervenfaser eine einzelne Cromatophore der Haut oder eine kleine Gruppe derselben in einem bestimmten Sinne beeinflusst." While such an explanation may prove useful by suggesting experimental procedure, the supporting evidence advanced is too meagre to give it value save as a working hypothesis.

Goldsmith (7½) reports further experiments upon *visual memory* in fish, claiming to have confirmed with three other species, her results of 1905.

New objects always frighten Gobius and Gasterosteus, but once having received food from forceps, the fish readily return, although still shy of a new object. She concludes that these fish retain "the memory of the aspect of objects along with that of their topographical situation."

Color experiments were carried on in two ways. 1. Colored papers were used on the bottom and sides of a glass basin.

Gobius show at first, as do the fish in Bauer's experiment, an aversion to the red, refusing to pass through the red passageway which they traversed freely while the bottom was sanded. After one hour, however, they make no discrimination. With Gasterosteus red was always "chosen" in preference to any other color; yellow, green and blue followed in order. Instead of indicating, as Mlle. Goldsmith claims, ability to distinguish *colors*, it would seem that the basis of discrimination is that of *brightness difference*, as has previously been pointed out by Hess.

2. Food was given from different colored forceps. The fish returned to the food-carrying forceps (the red) except when they were exactly transposed with the empty blue forceps. Then they came to the place where the red had been. The conclusion of Mlle. Goldsmith is that they have a *memory for colors*, as well as for position. The former is feeble and when memory of color and position conflict, the memory of place prevails.

The author found that the young of *Pleuronectes* were quite "curious" as to new objects. She accordingly took a record of the time necessary so to accustom them to a new object that they no longer noticed it. The time was not kept with exactness. Indeed, all through the experiment there is a deplorable lack of technique. Memory of color is claimed to have endured twenty-eight days, *i.e.*, twenty-eight days after having received food from the red forceps, one individual went directly to them on immersion of the red and blue forceps.

M. Piéron, in a discussion of the work of Mlle. Goldsmith, shows that "numerical precision" should have been sought as to the rapidity of the vanishing of the mnemonic trace, and also calls attention to the necessity of excluding from color experiments the luminosity variant. The lack of careful standardization of experimental conditions deprives the author's results of the value they otherwise might have. The paper deals as much with the formation and retention of habits as with vision proper.

Birds. Breed (2) shows that chicks in advance of any training respond positively to the more intense of two non-chromatic light stimuli. A similar result was not found in the case of chromatic light stimuli. Breed holds that this points to one

or both of the following conclusions: that (1) a difference exists between the chromatic luminosity values for the chick and those for the human being; or (2) the chick exhibits a qualitatively determined preference such as is apparent in some other animals. From results which the reviewer has in his hands, it is perfectly clear that Breed's first contention is contrary to fact, the chick's luminosity curve for monochromatic light being almost entirely similar to that of the human being. Whether we are forced to accept the second part of his conclusion depends upon the extent to which Breed and others have brought out all the remaining facts in the case.

The author finds further that chicks are able to select one of two colors at the brightness indifference point.

One of the animals gave convincing evidence of ability to make the circle-square distinction, while another animal quickly acquired the small-large habit—two circles eight cm. and five cm. in diameter respectively were used.

Mammals. Vincent (26) has given a very valuable table showing anatomical features of the mammalian retina. It is compiled from various researches dealing with the presence or absence of rods and cones, their relative number, distribution, the nature of the fovea and sensitive area, refraction, stereoscopic vision, etc.

Hoge and Stocking (12) in their study of motives have shown that the albino rat and hooded black and white rats can form a habit of responding positively to one of two white lights (when the intensity of one was two c. p., and the other sixteen c. p.). The number of trials required for the formation of this habit varied with the motive used, one animal requiring 490 trials, two others completing at the end of about 550. The authors show that in the discrimination of these lights, the offering of food with success and punishment (electric shock) with failure is more advantageous than the giving of either food alone or punishment alone.

Lashley (15) made a long series of tests upon albino rats to test their sensitivity to difference in form and size. In the first place he found that the introduction of a slowly moving sector in the pathway of one of the light stimuli produced no hastening of the habit of discrimination. He was enabled to get one animal to discriminate between vertical and horizontal

lines, and another to discriminate the thirty mm. from the fifty mm. circle. In testing for the threshold of form discrimination he found that one animal probably distinguished between two rectangles of twenty by thirty mm. with their long axes respectively horizontal and vertical, although forms more widely different (square and circle) were not distinguished.

Washburn and Abbott (28) in a carefully controlled research show that the rabbit can discriminate between the Bradley saturated red paper and Hering's grey Nos. 7, 14 and 15. Care was used to show that the discrimination was made in visual terms. Red was found to have a distinctly low stimulating effect. One series of experiments show discrimination between Hering's velvet black and Bradley saturated red, although some experiments carried out to test this latter conclusion fail to confirm the first set of experiments. The authors do not maintain that the above discriminations were made on any other basis than that of brightness difference.

The results obtained with saturated blue are not decisive; the animals, though, regularly distinguished it from Stoelting black. Here, too, the discrimination was probably made in terms of brightness. Several experiments tend to show that the brightness equivalent of the blue probably lies around Hering's grey No. 7. The authors hold that they have obtained some evidence to show that the rabbit is able to form the habit of choosing the darker of two impressions, irrespective of their absolute brightness. It is probable that the rabbit, while capable of using binocular vision, uses monocular more commonly.

Smith (24) tested the color responses of dogs. The tests were carried through completely only on one dog. The apparatus consisted of a large box suitably divided into home and trial compartments. Five shutters, each of which when pulled upward disclosed an opening for the exit of the animal, carried the stimulus. Food and punishment (consisting of electric shocks) were used as motives.

The principal stimuli employed were the Zimmermann colored papers; the most saturated red, blue, green, yellow, magenta and orange (Nos. c, o, k, g, a). The color work was controlled by the use of achromatic stimuli. For this latter work Nendel's greys were employed.

The author concludes that while certain of the dogs do pos-

sess the power to make rudimentary distinctions between the color, this function is a highly unstable one and cannot be supposed to play a part in the normal life of the dog. Furthermore, even when discrimination among the colors has been established, it may be lost easily through differences in luminosity and position.

AUDITION

Mammals. Shepard (22) finds that the cat discriminates articulate sounds, responding to its own name. The experimenter was in plain sight of the animal during the entire time of observation, sitting about a meter away in front of the cage. He worked with two cats. The name-reaction demanded in one case was the rearing up of the animal against the cage; while in the other case "the animal looked toward the food when its name was called." Learning in the latter case was considered as attained when the cat responded in this way to its name nineteen times out of twenty, and to "no feed," the counter phrase he used, four times out of twenty.

Swift (25) reports some experiments upon a dog trained to take meat at a low tone and to refrain from taking it at a high tone. After training, the left temporal lobe was removed; training was then resumed and when the reactions were re-established, the right temporal lobe was removed. The author reports that even after both lobes have been removed the dog can be retrained (slowly) to distinguish between the two tones used in the original training and also to establish new associations.

It is very doubtful if any of the work recently reported by Kalischer and by Swift will bear critical scientific examination. Johnson, in a recent monograph (*Behavior Monograph No.* 8) discusses their experiments at length. The reader is referred to this place for critical evaluation of such studies.

Johnson (14), in a review of Oscar Pfungst's report, "Der sprechende Hund," accepts Pfungst's explanation of the claims made by the dog's owners. The animal was reported to possess a vocabulary of eight words: *Don, Hunger, Haben, Kuchen, Ruhe, Ja, Nein,* and *Haberland,* and with these words to answer accurately certain questions as, "*Was hast du?*" "*Hunger.*"

Doctor Pfungst with Professor Vasseler and Doctor Erich Fischer investigated the behavior of the animal, a German

setter seven years old, and found, first, that his vocabulary consisted of just three sounds: one vowel, of a value lying between *o* and *u*; one guttural-aspirant like the German *ch*; and one nasal, lying between *n* and *ng*. A sound made by the dog, expressed by *ch-u-ng-uo*, is easily interpreted by suggestible hearers as "*Hunger*." They also discovered that he always responded, with the various combinations of these sounds that he used, in the same order, beginning with "*Don*" and ending with "*Ruhe*" no matter in what order the questions were put to him, so that he might desire "*Hunger*" be called "*Kuchen*" and so on.

Doctor Pfungst concludes that the speech of Don is to be regarded properly as the reproduction of vocal sounds which produce illusions in the uncritical hearer, who makes no effort to distinguish between perception and imagination and ignores the rôle played by imagination. Johnson adds that, "we may expect animal lovers to continue to read their own mental processes into the behavior of their pets," and "scientists of a certain class to continue * * * to proclaim * * * that they have * * * demonstrated the presence in lower animals of intelligent imitation and other extremely complicated mental processes."

CUTANEOUS SENSITIVITY

Amphibia. Babák (1) has devised a very sensitive method of studying the sensitivity of the frog to various stimuli. He has found that the breathing rhythm of a frog with the fore-brain removed proceeds with machine-like regularity, interrupted only when the animal is stimulated and resumed shortly after the stimulating agent is removed. In the maimed frog lung ventilation also occurs only after stimulation. In his first paper upon the sensitivity of the frog, the second of a series of studies upon the breathing rhythm, the author takes up the sensitivity of the animal to temperature as determined by changes in the breathing rate. The animals used were completely recovered from the shock resulting from operation upon the brain. The temperature stimuli were applied by means of a thermaesthesiometer held at a distance of one mm. from the animal's skin. The actual temperature changes in the skin could be judged only approximately. During experimentation great care was required to avoid auditory and tactile stimuli, etc.

The specimens studied were found to be sensitive to slight changes in either direction from the physiological zero point. No means of measuring these changes were found, but the same stimuli were applied to human subjects, and this leads to the conclusion that the frog's skin is at least as sensitive to temperature as that of man. The head was found to be more sensitive than the sacral and lumbar regions.

Stimulation with a temperature above the physiological zero caused an increase in the rate of breathing, with one below a decrease. This was not explainable as a change in physiological rate due directly to change in the temperature of the organ systems, since the change in temperature affected only a small area of the skin. Hence the author concludes that there is no direct energetic relation between the direction of change in the stimulus and the direction of change in the reaction. Moreover, all temperature stimuli caused lung ventilation, reactions in the same sense or direction. In spite of this last fact and the morphological results of the investigation of the temperature sense in man, the author is inclined to support the old assimilation and dissimilation theory of Hering as furnishing the best explanation of the difference in the sense of reaction. He asks "Wurde es vielleicht allgemein gelten, dass eine jede noch so kleine Energiezufuhr in das System eine Beschleunigung, eine jede Energieausfuhr eine Herabsetzung des Atemrhythmus bewirkt?"

Fish. Parker (18) reports a series of experiments upon the common chemical sense of Ammocoetes and of Amiurus and considers the structural and phylogenetic relations of this sense to those of smell and taste. He finds that the skin of Ammocoetes is sensitive to HCl, NaOH, NaCl, and quinine in solution, but not to cane sugar. The solutions were brought in contact with the skin by means of a pipette and their effect judged by the animal's movements. Three regions of the body were studied, the head, the mid-trunk, and the tail. The head was found to be far more sensitive than the tail and the latter somewhat more sensitive than the trunk. Experiments with Amiurus gave essentially the same results but with no difference in sensitivity between the mid-trunk and tail. Sectioning of the olfactory crura did not affect the reaction, nor was the sensitivity destroyed by severing the lateral line nerves and lateral accessories. This limits the sensory

mechanism to the terminations of the spinal nerves in the epidermis and assures that the common sense is independent of the taste buds which are scattered over the surface of the body and are innervated by the lateral accessories.

By an examination of the effects of various substances Parker concludes that the ions stimulating the common chemical receptors are the same as those stimulating the human taste buds, and that taste and the common chemical sense are closely related in the vertebrate both with respect to their sensitivity and the nature of the stimuli received. Smell, on the contrary, he finds in fish, as in the land vertebrates, to be much more sensitive to weak stimuli, and to serve, probably, as a distance receptor.

The author differs from Herrick and Sheldon in holding that the olfactory sense presents the primitive form from which the others have been derived. He is led to this view chiefly by the similarity of the olfactory neurone to sensory cells found in invertebrates.

In a brief preliminary note Shelford and Allee (21) describe their apparatus for the study of reactions of fish to solutions of gases and solids and review the results obtained by its use. The device consists of a rectangular tank with an intake at each end and an outlet in the middle. Waters differing in their dissolved contents can be admitted at the two ends, thus forming, in the middle of the tank, a gradient to which the fish react. Eight species of fish were studied. They were found to give indefinite or slightly negative reactions to changes in oxygen pressure and to slight reductions in the salt content. There was no evidence of reaction to nitrogen. All the fishes avoided water containing a per cent. of carbon dioxide greater than that to which they were accustomed (to increases of from five to sixty cc. per liter), and when an increase in carbon dioxide was accompanied by a decrease in oxygen the negative reactions became very pronounced.

The authors conclude that, except in cases of strongly alkaline waters, the content of carbon dioxide furnishes the best single index to the suitability of a water for fishes. The experiments seem to have been well controlled by the use of a second tank in which only one quality of water was used.

EXPERIMENTAL AND OBSERVATIONAL STUDY OF INSTINCTS

Amphibia.   Hargitt (10) gives some interesting data upon food taking and hibernation in two species of tree frogs (*Hyla versicolor* and *H. arborea*).   In regard to food taking he says it is evident that the tree frog responds only to moving objects. A motionless spider may remain for hours in the cage without being disturbed; the moment it becomes active, however, the frog will seize it.   The frog usually leaps to take its prey, rarely stalking it.   It waits until the prey is within leaping distance, which may mean several feet.   It springs upon the victim, taking it with ease and rarely missing.   Its prey apparently is not seen at close range.

In regard to hibernation the author says that the laboratory specimens show no tendency to hibernate so long as normal temperature is maintained.   Several specimens were taken into a cool, damp cellar, the last week of December.   Very soon after the change they showed signs of dormancy and burrowed (this consists of *backing*, using the hind feet and sharp posterior end of the body) under the mass of debris.   The experiment upon hibernation was not completed because of the death of the animals.

In regard to color changes, it may be said that there is a wide variation in the native habitat even where the environmental conditions, so far as could be observed, are the same. Experiments show that, as a rule, light tends to bleach the skin and rob it of its pattern.   Darkness seems to have no positive effect upon the color change or skin pattern.   Some exceptions to the lightening effect upon the skin of light are to be found. In some cases a greenish color was induced by sunlight which persisted for days.   High temperature seems to act much as does strong light—in general producing lightening of the skin. There are also some exceptions to this rule.   A low temperature seems to have no effect upon color change.   Contact stimuli seems to be equally void of effect upon color change.

Reptiles.   Ruthven (20) makes some interesting observations on the breeding habits of Butler's garter snake (*Thamnopsis butleri Cope*).   He concludes that the breeding season is about a month long, its initiation depending on the climate, being in Southern Michigan from the latter part of March over most of April.   In the case observed by him courtship lasted for five days, copu-

lation for two hours and fifteen minutes, beginning about noon, and the period of gestation was 144 days long.

He also concludes that the so-called snake piles are due to the sexual impulse and not to the social, for when the sex impulse was at its height in the case observed, five males were at the one time endeavoring to copulate with one female.

Birds. Haggerty (9) presents a clear case of the first performance of a particular instinctive act of a young bird. A young sparrow hawk, having fallen from its nest with injury to its wing, was removed to the laboratory and reared by hand. It throve and became very gentle. On the third day a small piece of roast beef was placed in the cage; the hawk seized the meat with one foot, sinking its claws viciously into it. Its feathers became ruffled and its wings outspread. It fluttered about the cage, still holding to the meat. It continued for some time to strike its booty with its bill, the free foot and its wings. Apparently the larger the piece of meat and the greater the hunger of the bird, the more pronounced was the reaction.

Craig (7) shows that the blond ring-dove (*Turtus risorius*) does not instinctively give drinking response to the sight or sound of water nor to the touch of water on distal parts of the body. The young dove first gets its bill in the water by pecking at objects in the water. The contact of the fluid on the skin inside the mouth releases the further steps of the act of drinking. Birds will imitate pecking of parents or other birds, but do not imitate the act of drinking as such.

The same writer (6) has made observations upon the manner in which young birds break out of the egg. The results of these observations confirm those obtained by the early naturalists. The author summarizes these as follows. The bird chips the egg a little at a time with the bill; as it does so it turns around inside the shell. the axis of rotation coinciding with the long axis of the shell. As a consequence of this form of action, the egg is chipped around the large end in almost a perfect circle. After the circle has been almost or quite completed, the bird pushes in such a way as to force apart the two sections of the shell.

Phillips (19) gives the results of some observations on the inheritance of wildness in "English mallards," a game bird long bred on the English preserves. Young ducks of pure

strain were hatched under hens. These ducklings were found to be quite tame from the first and as easy to manage and rear as the common duck. Their instincts, however, especially those of feeding, differed widely from those of the common duck. On the other hand, the young of back crosses between the common tame mallards and pure wild black ducks (*Anas tristis*) gave other results. One such cross gave young which showed three-quarters *A. tristis*, while in two other crosses the young were only one-fourth *A. tristis*. The three-quarter *A. tristis* showed exceeding wildness. They were hard to manage and were reared with difficulty, but their dispositions changed with age and they became much more like ordinary ducks.

Mammals. Slonaker (23) undertakes to give some expression of the normal activity of the albino rat from birth to death. In studying normal activity at different ages he used a cylindrical cage which revolved upon a stationary axle. On the axle were fastened the nest box, the food box, and the drinking pan. These parts were arranged in such a way that the animal had to step to the floor of the revolving cage in order to pass from the food or water receptacle and vice versa. The weight of the animal caused the cage to revolve whenever he stepped upon the inner surface of the cage. A recording device was installed which indicated the number of revolutions made by the cage and their temporal distribution. Eight young rats were kept with the mother until twenty-eight days of age. Four were placed in the apparatus described above, where they remained constantly, except for weighing and cleaning of the cages, etc., until death. A separate revolving cage was provided for each animal. The other four rats were used as controls. They were placed in separate stationary living cages of the ordinary variety. Several important results are claimed for this research. The daily activity increases rapidly during the first third of the life period, after which there is a gradual decrease until death. During the period of youth and that of old age, the active moments are well distributed over the whole twenty-four hours, whereas, during the prime of life, activity is confined principally to night and rest to day. The rats are thus nocturnal. In regard to the amount of work done, it was found that three-fourths of the total amount done was done before middle age was reached. During the last thirty per cent. of life, only one-

eighth of the total work was performed, whereas, during the first thirty per cent. of the life span, three-eighths of the total work was done.

Unexercised animals (controls) reached their maximum weight at an early period. At corresponding ages the controls had a greater absolute weight than the exercised rats. The unexercised animals lived longer than the exercised ones.

Slonaker's conclusions probably have not the universality he claims for them. In the first place, the activity necessary to cause the cage to revolve cannot be taken as an index of all other forms of activity. Probably many other forms of activity have a far different type of life history than that involved in causing the cage to revolve. Further, Slonaker's work tells us really nothing of the relative amounts of work the animals can do at different ages. This phase of the subject is not touched upon by him. He sets the adult rat to revolving a mechanism so delicate that a twenty-eight days old animal can work it. His records show not the amount of work the animal can do at different ages, nor even the relative lengths of time during which this activity would take place under slightly different conditions. In other words, Slonaker is dealing rather with the temporal aspects of a certain type of activity. Often the distribution of time in running is misleading, too, because of the unequal effort called forth between young and old. The rat at twenty-eight days is probably working up very near to his maximum limit of effort in causing the cage to turn; he may leave off at any time by reason of exhaustion; whereas the adult rat may cease activity at the end of two hours merely because a stronger stimulus impels him elsewhere. It seems to the reviewer to be hard to draw any legitimate conclusion from Slonaker's work until there can be some suitable method of getting a measure of fatigue, etc.

Coburn (3) records some specimens of the house mouse (*Mus musculus*) which were able to sing in the sense in which that act has been described by Lee and Brehm. The "singing" resembles the soft chirp of a bird; it is best described as a rapid, whole toned trill involving the tones of c and d. The clang character is similar to that of flute or pipe tones.

Cole (4) summarizes his observations on the instincts of raccoons and their use of the senses. He gives the following as

a partial list of the more important instincts. Certain *vocalizations*, such as the whimper and the purr; *sucking*, which is active until the young are four months old; *creeping; climbing*, the latter beginning to appear at a very early age. At one month of age it is able to sustain its own weight with one paw by clinging to a support; in this instinctive attitude it is difficult to remove the young animal from bushes, etc. *Playing*, with parts of its own body; rolling a small object between the forepaws; engaging in mock combat; pretence of biting the hand, etc. *Following; fear; anger; curiosity; dipping food in water;* the sex group does not appear until the twelfth month.

In drinking they lap water or milk with the mouth close to the fluid. When heated, they pant much like dogs, with tongue slightly protruded. In sleep, one position assumed is that of lying on the back with the fore paws over the eyes; another is rolling the body into a ball with the top of the head placed flat on the floor between the forepaws.

ORIENTATION

Birds. Ménégaux (17) proposes to study the migrations of the European quail in order to determine the route of migration and the winter feeding grounds. It is known that the birds cross the Mediterranean and arrive in Morocco, Algeria, Tunis and Tripoli in autumn, but beyond this there is little definite knowledge of their movements. The experiment planned will involve the banding of 500 birds in France for the study of the autumn France-to-Africa migration; of 500 in Algeria and Tunis for the route of return to France; and, finally, of 500 in Egypt to determine whether the Egyptian birds return to France or go into Asia Minor and the region of the lower Danube. The author expects that the twelve and a half per cent. of returns usually obtained from marked birds will give sufficient data to establish the lines of migration and the regions in which it will be necessary to protect the quail in order to maintain the supply in France. While this work is undertaken chiefly from the point of view of economic zoölogy, it may furnish data upon orientation of interest to the student of behavior.

Mammals. Cornetz (5) compares the method of orientation in the ant and the rat. He considers first an experiment of

Szymanski's in which a rat learned a very simple maze in five trials, shortening its path somewhat at each trial. His analysis of this experiment is something of a mental atavism. The rat was trained to run through the maze to a dish of water, and Cornetz, after describing the first two trials of the experiment, proceeds as follows: "He (the rat) thus recognizes that the water dish is a little to the left (of the entrance to the maze); yet I do not feel the need of supposing that he wished to suppress the useless movements of his former path." After the rat has made two more trials:—"Now the rat has grasped the position of the water dish in space much more clearly, confirming the path of the third trial by that of the fourth, and is able to go directly to the water. It is not, it seems to me, for the useful purpose of reaching the water dish more quickly that the rat shortens his fifth path but because his representation (conscious?) of the position of the dish has finally become clear. I believe that for every being that gives evidence of memory the external world, space, has the form that the being's sensations give it. The external medium is projected into the being in the form of a complex of persistent images." Such speculation scarcely needs comment. It offers nothing helpful in the interpretation of behavior. The author was evidently led astray by the misunderstanding which he has expressed in the following quotation. In discussing the dropping of useless movements in habit formation, he says, "According to this finalistic idea (dropping of useless movements) the rat, knowing by its first trial the position of the water dish, for it must know this in order to modify its path, suppresses its useless movements little by little." This statement reveals an entirely false conception of what is meant by the dropping of useless movements. The expression has been employed to describe what is actually observed in habit formation and to avoid exactly what Cornetz reads into it, the implication that there is conscious purposiveness in the process.

But all this is aside from the chief object of the comparison, which is to show that the rat depends upon the relative position of objects for its orientation, and that the ant probably does not. The first may be admitted without question, but it is extremely doubtful whether the ant possesses a sense of absolute direction in space as the author is inclined to believe. The

evidence advanced is quite inadequate to prove that the ant's method of orientation is in any way different from that of the rat. In the author's various papers, dealing with ants, cases are given in which each of the sensory factors, possibly active in orientation, smell, vision, touch, kinaesthesia, magnetic sense, etc., seem to have been eliminated singly, but no case of correct orientation is recorded in which vision and the muscle sense were eliminated together; indeed the author does not consider the possibility that two or more senses may contribute somewhat independently to the sense of direction. Until such possibilities have been tested thoroughly, it seems unnecessary to invent a sense of absolute direction, "inconceivable," though not necessarily "impossible."

IMITATION

Mammals. Warren (27) reports a case of delayed imitation in the cat. One of two pets formed, through efforts of his own, the habit of climbing into the author's lap, then to his shoulder, and out over his outstretched arm to a piece of meat held on a fork. The companion of this cat made no attempt for months to perform this trick, although watching the trained animal feed in this way daily. This second cat had often been coaxed to make the effort. One day, however, after watching the trained animal feed, he suddenly, of his own accord, sprang on the author's lap, out over his arm and seized the piece of meat. After this he became the sturdy rival of the cat which had first learned the trick.

Hunter (13) finds that the white rat can learn by being "put through" an act. As a part of the daily routine of experiment of the group of rats it was found necessary to deposit each animal, after completing his quota of work, in a small box. This was accomplished by lifting the animal up and dropping him through a hole in the top of a box situated on the table which held the living cage. The animal remained in this box until all the members of the group had been worked with, after which the group as a whole was removed to the living cage and there fed. On the two hundred and fourth day after experimentation had begun the door of the living cage was left open by accident. Two of the five rats climbed to the top of the small box and dropped to the floor of their own accord and

remained there as was their custom during the regular routine of experimentation. A regular set of tests was then initiated. Hunter was able to obtain several performances of a similar kind.

HABIT FORMATION

Amphibia. In connection with his breeding experiments upon the Mexican axolotl (*Amblystoma tigrinum*) Haecker (8) has made a study of learning and retention in relation to sexual and other changes in the individual. The animals were trained to distinguish between pieces of meat and wood of the same size, drawn before them slowly in the jaws of a long pair of forceps. The receptors involved in the discrimination were not very thoroughly analyzed, the author resting content with the statement that vision plays a very slight rôle, while a "special function of the oral sense" and apparently the perception of water currents are the chief factors in the reaction. The question of the impulse to the reaction, hunger, has, on the contrary, been treated at great length. Considerable variation in the degree of hunger was found from day to day, seemingly associated to some extent with atmospheric conditions, but it was found that after the animals had been trained for a month the errors made had little relation to the degree of hunger.

The animals learned readily to distinguish between the meat and the wood and to avoid the latter. The most noteworthy thing about the learning curves is the rhythmic appearance of periods in which numerous errors were made long after perfect learning had been reached. Thus, in the case of a black female which was studied for two and a half years, a large number of errors were made in June, 1910, October, 1910, December, 1910, May, 1911, and the winter of 1911, while the intervening periods were almost without error.

Averaging his results, the author finds that the periods of error are distributed about two maxima, one in summer, one in winter. Once the animals had learned to distinguish between the meat and the wood the errors were not increased by rather long interruptions of training or by fluctuations in the degree of hunger. The two maxima agree with the periods of greatest sexual activity and the author believes them to be the result of the latter; that the physiological changes occurring during

the breeding season affect certain psychic functions not directly connected with reproduction.

Individuals differed considerably in the time of learning and the frequency and extent of the periods of error. Young animals (nine months old) learned with far greater difficulty than mature ones. Among adults three types were distinguishable with respect to the time of learning and retention. Experiments are still in progress to determine whether these types are of selective and hereditary value.

Mammals. Hicks and Carr (11) took up the comparative abilities of human adults, children and white rats to learn a maze. The maze for the man was placed out of doors; its dimensions were fourteen by twenty feet; the alleys were two feet in width, the true path seventy-eight feet in length, complicated by nine *cul de sacs*. The human subject had to run the maze blindfolded. One group of rats learned the Hampton Court maze and another a maze especially constructed by Carr. The results of these experiments show that rats can learn a maze in a fewer number of trials than the human beings. The authors, however, are cautious about adherence to the letter of this conclusion, since the mazes were different and since the criteria of mastery were different, and, further, since only a very small number of individuals were tested. This paper further takes up rather thoroughly the relative ability of the different animals to eliminate errors, distance and excess of time, the relative variability of the three groups, and the relation of the learning curves to intelligence. Under the latter head we find the most complete discussion we have at present of the significance of the form of learning curves. Especially discussed is the significance of the sharp initial drop we find in most learning curves. Since the argument is rather closely connected, the reader must be referred to the original paper.

REFERENCES

1. Babák, E.   Ueber die Temperaturempfindlichkeit der Amphibien. *Zeit. f. Sinnesphysiol.*, **47**, 34-45.
2. Breed, Frederick S.   Reactions of Chicks to Optical Stimuli. *Jour. Animal Behav.*, **2**, 280-295.
3. Coburn, Charles A.   Singing Mice. *Jour. Animal. Behav.*, **2**, 364-366.
4. Cole, Lawrence W.   Observation of the Senses and Instincts of the Raccoon. *Jour. Animal Behav.*, **2**, 299-309.
5. Cornetz, Victor.   Comparison entre la prise d'une direction chez un rat et chez une fourmi. *Bull. Inst. gén. psych.*, **12**, 357-366.
6. Craig, Wallace.   Behavior of Young Birds in Breaking Out of the Egg. *Jour. Animal Behav.*, **2**, 296-298.
7. Craig, Wallace.   Observations on Doves Learning to Drink. *Jour. Animal Behav.*, **2**, 273-279.
7½. Goldsmith, M.   Contribution à l'étude de la mémoire chez les poissons. *Bull. Inst. gén. psych.*, **12**, 161-176.
8. Haecker, Valentine.   Ueber Lernversuche bei Axolotln. *Arch. f. d. ges. Psych.*, **25**, 1-35.
9. Haggerty, M. E.   A Case of Instinct. *Jour. Animal Behav.*, **2**, 79-80.
10. Hargitt, Charles W.   Behavior and Color Changes of Tree Frogs. *Jour. Animal Behav.*, **2**, 51-77.
11. Hicks, Vinnie C. and Carr, H. A.   Human Reactions in a Maze. *Jour. Animal Behav.*, **2**, 98-125.
12. Hoge, Mildred A. and Stocking, Ruth J.   A Note on the Relative Value of Punishment and Reward as Motives. *Jour. Animal Behav.*, **2**, 43-50.
13. Hunter, Walter S.   A Note on the Behavior of the White Rat. *Jour. Animal Behav.*, **2**, 137-141.
14. Johnson, Harry Miles.   The Talking Dog. *Science,* N. S., **35**, 749-751.
15. Lashley, K. S.   Visual Discrimination of Size and Form in the Albino Rat. *Jour. Animal Behav.*, **2**, 310-331.
16. Loeb, Jacques.   Die Bedeutung der Anpassung der Fische an den Untergrund für die Auffassung des Mechanismus des Sehens. *Centralb. f. Physiol.*, **25**, 1015-1017.
17. Ménégaux, M. A.   Les Migrations des Cailles. *Bull. Inst. gén. psych.*, **12**, 92-94.
18. Parker, G. H.   The Relation of Smell, Taste and the Common Chemical Sense in Vertebrates. *Jour. Acad. Nat. Sci. Phila.*, **15**, 219-234.
19. Phillips, John C.   Note on Wildness in Ducklings. *Jour. Animal Behav.*, **2**, 363-364.
20. Ruthven, A. E.   On the Breeding Habits of Butler's Garter Snake. *Biol. Bull.*, **24**, 18-20.
21. Shelford, V. E. and Allee, W. C.   An Index of Fish Environments. *Science*, N. S., **36**, 76-77.
22. Shepard, W. T.   The Discrimination of Articulate Sounds by Cats. *Amer. Jour. Psych.* **23**, 3.
23. Slonaker, J. R.   The Normal Activity of the Albino Rat from Birth to Natural Death, Its Rate of Growth and Duration of Life. *Jour. Animal Behav.* **2**, 20-42.
24. Smith, E. M.   Some Observations Concerning Color Vision in Dogs. *British Jour. Psychol.*, **5**, 119-202.
25. Swift, Walter B.   Psychological Results in Reaction to Tone Before and After Extirpation of the Temporal Lobes. *Jour. Animal Behav.*, **2**, 225-228.
26. Vincent, S. B.   The Mammalian Eye. *Jour. Animal Behav.*, **2**, 249-255.
27. Warren, Edward R.   Delayed Imitation in a Cat. *Jour. Animal Behav.*, **2**, 222-224.
28. Washburn, M. F. and Abbott, Edwina.   Experiments on the Brightness Value of Red for the Light-Adapted Eye of the Rabbit. *Jour. Animal Behav.*, **2**, 145-180.

LOEB'S "THE MECHANISTIC CONCEPTION OF LIFE"[1]

JAMES R. ANGELL
The University of Chicago

This volume brings together ten essays published by the author during the years 1891–1912. The absence of fresh material is more than made good by the convenience of the compilation for readers who desire access to Dr. Loeb's views and who cannot well follow his brilliant but scattered writings in the scientific journals.

The book takes its title from the opening essay, which is a general presentation of the thesis that life phenomena can all be adequately explained in physico-chemical terms, and that no other terms can ever be final. The remaining essays afford specific instances of the application of the thesis, and cover such topics as tropisms, the physiology of the central nervous system, pattern adaptation and physiological morphology, the process of egg fertilization, artificial parthenogenesis, the rôle of salts in the preservation of life, and the influence of environment on animals. In each case experimental evidence is adduced to show how the special phenomena under consideration may be explained by chemical or physical principles.

Only two of the essays contain material directly related to the interests of this journal, i.e., that on tropisms and that on facts and conceptions concerning the comparative physiology of the central nervous system. We shall, therefore, confine our attention to certain issues raised in these chapters, and first consider the case of the tropism. Be it said at once that we waive all discussion of the purely physiological and zoölogical questions upon which the authorities are at variance. It is well understood that Loeb's view of tropistic reactions does not enjoy universal support among zoölogists. For the present purpose we may assume the theory to be correct.

Three propositions substantially express Dr. Loeb's main contentions in the matter. (1) In tropistic organisms, owing to the

peculiar connection of sensitive surfaces with muscle tissue, if physical or chemical stimuli to which such animals are susceptible attack one side of the organism more violently than the other, the muscles of the two sides will be unequally innervated. (2) In animals possessing symmetrical anatomical disposition of muscles this unequal innervation will result in orienting movements tending to bring the organism into a position where the stimulus falls evenly on the two sides, i.e., into a position pointing toward or away from the source of the stimulation.   (3) It should be the aim of psychology to reduce all the forms of psychic behavior to the same essentially physico-chemical explanations as are afforded by the knowledge of tropisms.   Dr. Loeb's own words on the third point may be quoted: " To me it is a question of making the facts of psychology accessible to analysis by means of physical chemistry."   (P. 61).

This pronouncement, which a decade or two ago might have occasioned considerable agitation, will hardly cause a flutter in the psychological breast today.   The notion that the practically useful type of explanation of mental events is to be found in terms of neural activities is now almost universally accepted among experimental psychologists.   Obviously it is in physical and chemical terms that the final analysis of these neural processes is to be given.   The fact that we seem today to be a long journey away from any adequate physico-chemical knowledge about the inner workings of the nervous system detracts not a whit from the theoretical soundness of the position.

The psychological issue which is really raised by this doctrine, although Loeb does not explicitly enter upon it, concerns the necessity for a thorough-going analysis of the psychical facts themselves, and the methods of executing such analysis. To be sure he remarks (speaking of comparative psychology): " But I believe also that the further development of this subject will fall more to the lot of biologists trained in physical chemistry than to the specialists in psychology or zoölogy * * * ." (P. 61).   How far, however, he recognizes a necessity for a technique of mental analysis as a preliminary to his process of chemical and physical explanation is not clear.

In the case of human behavior at least the need for strictly psychological analysis seems to the present writer so obvious as to be almost truistic, and yet many intelligent persons, not for-

getting some of our medical friends, appear to believe that the psychology of common sense, the kind which supposedly comes by nature, is all that is essential. It appears well-nigh incredible that anyone unfamiliar with the intricacies of the memory processes, as modern psychological analysis has revealed these, should seriously propose to give an adequate physical or chemical explanation of the memory function. It is precisely the peculiarities so disclosed which require explanation. If the physico-chemical explanations of the future are to apply in a vague general way to memory activities loosely conceived and imperfectly analyzed and described, if they are not to afford us an understanding of specific detail, we may find them interesting and suggestive, but in effect we shall be substituting one set of essentially metaphorical terms for another, and our actual advance over present conditions will be relatively slight.

What is true of memory is equally true of auditory and visual sensation, of emotion, of reasoning, of volition and all the rest of the fundamental mental operations. The facts to be physico-chemically explained themselves require an adequate technique of discovery and description. To supply this must be the business of psychology, or some more worthy successor by whatever name known. Psychological facts are no more directly accessible to physical and chemical analysis than they are to deep sea soundings.

What methods are to be accepted and developed for this purpose remains to be determined. This is not the place to discuss the matter. Suffice it to remark that the oldest of the psychological methods, i.e., introspection, is at present under severe fire.

Dr. Loeb's widely quoted analysis of the activities of the central nervous system raises a host of pregnant questions of which only one may be touched upon here, to wit, the conception of "associative memory." "Consciousness is only a metaphysical term for phenomena which are determined by associative memory. By associative memory I mean that mechanism by which a stimulus brings about not only the effects which its nature and the specific structure of the irritable organ call for, but by which it brings about also the effects of other stimuli, which formerly acted upon the organism almost or quite simultaneously with the stimulus in question." (Pp. 73-4).

So far as the issue is one of terms merely, a large latitude should be accorded to personal preference, and if Dr. Loeb finds "associative memory" a more agreeable term than "consciousness," no one may justly object. But if it be supposed that by the use of the phrase "associative memory" any greater insight has been gained into the organic happenings commonly called "conscious," a demurrer may justly be entered. Psychologists have used the term consciousness as a general rubric under which to subsume not only memory and association, but also perception and inference and pleasure-pain and attention, to mention only a few of many constituents. It may be correctly asserted that they have often used the term as though it applied to a specific agent, and have thereby foisted a spurious explanation of certain phenomena upon an unsuspecting public. Not all have fallen into this pit. But even granting this shortcoming, it is not clear that an insight into the essential physico-chemical causes of behavior is any more exact or more tangible when we refer a phenomenon to associative memory, than when we refer it to conscious action. In either case we remain in profound ignorance of the physical and chemical changes which permit that marvelous achievement—the recall of past experiences. We may and do postulate such a property of brain action, but its chemical basis remains as inscrutable when we call it associative memory as when we use the older phrase "organic memory," or when we label it in some other fashion.

One must not impute to Dr. Loeb any indisposition to recognize the force of this contention. He may, or may not, agree with it. But it is fair to call attention to the danger to which his conception exposes him, the danger of failure to take into account the complexities of conscious behavior which psychological analysis has revealed and which await the physico-chemical explanations he so earnestly seeks. The danger is perhaps as great as any to which psychologists are exposed with their meagre knowledge of physical chemistry. It is the danger of a treacherous over-simplification. To make consciousness synonymous with associative memory is thoroughly justifiable if the one really includes all that is in the other. But if, as is all too easy, one has attention fixed largely or solely upon the purely memorial part of the process, much will be overlooked which is not memory at all in any proper sense, and much which requires explanation and interpretation in a peculiarly urgent manner.

On the whole, then, psychologists will wish to speed the day
when psychic behavior can be analyzed exhaustively and cor-
related with the chemical and physical changes in the brain
upon which it depends. But there will be more rather than
less need in that day for a thorough-going dissection of the
psychic process itself, carried out by such methods as may be
found adequate. Nor will there be any more eager searchers
for accurate knowledge of the brain activities which render
memory possible than will be found among the psychologists.
But they will hardly feel that a metaphor like 'associative
memory' is a satisfactory substitute for what is thus desider-
ated. Even when the term is applied to strictly physical and
chemical activities, it tells us nothing we did not already know.
When Dr. Loeb, or any one of his scientific colleagues, is really
able to give us the inner chemical and physical facts of brain
action, our debt, already great and gladly acknowledged, will
be immensely increased.

MORGAN'S "INSTINCT AND EXPERIENCE"[1]

EDWIN G. BORING
Cornell Univresity·

This book is an outgrowth of its writer's discussion of Instinct
and Intelligence in the Symposium held on those subjects in
London in 1910 (*cf. British Journal of Psychology*, 3, 1910, 219).
In the first half of the book the writer discusses the "nature
of instinctive behavior and its accompanying instinctive experi-
ence," and then, in the second half. he goes on to present a
doctrine of experience, which he regards as the necessary out-
come of his theory of instinct, and to which he brings support
from many quarters. The views of McDougall, Myers, Stout,
and Driesch are repeatedly discussed throughout the volume,
while, in addition to other numerous references, an entire chapter
(Chap. VII) is devoted to Bergson's philosophy of instinct. The
whole presentation has a much more directly logical and episte-
mological, and a much less directly psychological, bearing, than
the title and the author's name would lead one to expect.

The first two chapters are devoted to the discussion of instinct
and of instinctive behavior. The latter is said to be "congeni-
tally determined" and "practically serviceable on the occasion
of its first performance" (p. 22), whereas the former is instinc-
tive behavior together with the experience that is correlated
with it. Although "practically serviceable," instinct is not
perfect, and from the first it is subject to modification by intel-
ligence. Intelligence is distinct from instinct with regard to
meaning, for the successive phases of the instinctive process in
its first occurrence possess "primary meaning," inherent in
their mere succession, while upon repetition of the process there
is anticipation or "pre-perception" of the as yet unrealized
phases by revival of the first occurrence,—an anticipation which
supplies "secondary meaning" to the process and characterizes
it as intelligent. A vaguely conscious "pre-perception" may
accompany the first occurrence of the instinctive performance,

---

instinct and intelligence thus occurring together from the very
first, and being separated only by abstraction.

The distinction between instinct and intelligence is made
more concrete by reference to the nervous processes involved
(Chap. III). The author finds three kinds of behavior: (1) the
reflex, which is unconscious and is correlated with processes in
the spinal cord; (2) instinctive behavior, which involves "suf-
fused awareness" and is connected with processes in the sub-
cortical centers, and (3) intelligent behavior, which is antici-
patory and is confined to cortical processes. He reviews the
work of Sherrington, Foster, Schrader, Goltz, and Pagano, and
bases his conclusions upon the differences in behavior between
normal, decerebrate, and spinal animals.

In Chapter IV we are told of "innate tendencies" or "inher-
ited dispositions," which are due to "congenital connections in
cortical centers;" just as instinctive behavior is dependent upon
"congenital connections in sub-cortical centers." There are a
large number of innate tendencies, which include inherited
capacities for acquirement. The vague "pre-perception," which
accompanies the first occurrence of instinctive behavior, is due
to an hereditary cortical disposition.

The next two chapters deal with the nature of experience and
its relation to natural history. Experience, both as "that which
may be experienced and as the process of experiencing," is held
to be everywhere interrelated and to be grounded throughout
in nature. The unitariness of all experience is not violated by
the appearance of new orders in history, for these, although
unpredictable, are merely new syntheses in experience.

The last chapter is entitled "Finalism and Mechanism." The
writer defends mechanism in the sense that all natural processes
are determined and can be correlated. He does not hold, how-
ever, that any process can be expressed in terms of any other
process, and distinguishes four principles of interpretation,—
mechanical, mechanistic (physical and chemical), organic, and
psychological. The first two,—possibly the first three,—it may
perhaps be possible to merge; the last quite probably must
remain distinct. Finalism is accepted only in such cases as
involve anticipatory consciousness.

On the whole, the author has succeeded in giving a clear, if
sometimes repetitious, presentation of his own doctrine of "the

intra-mundane philosophy of experience." One could wish, however, that the presentation were a little less personal, that it contained fewer references to several of the author's associates, and more references to less immediate philosophical sources. To pass over the doctrines of interactionism and psychophysical parallelism in half a dozen pages seems hardly fair. One wonders, also, whether a discussion of instinct is the best starting-point for the presentation of a doctrine of experience. The first four chapters might be more intelligible if they followed the last four; and at best it is a question whether there is any gain in presenting the two topics, instinct and experience, in the same volume.

In the discussion of instinct, one is prone to question repeatedly the positive correlation of mental and neural processes. Even granting all the other correlations and the necessity for the "pre-perception" with the first instinctive performance,—a concession which it is not likely that most critics would make,— one is still inclined to wonder in just what way the "pre-perceptive disposition" is proven to be cortical. And yet it is on this fact that the whole theory of instinct depends.

SCHNEIDER'S "TIERPSYCHOLOGISCHES PRAKTIKUM IN DIALOGFORM"[1]

MADISON BENTLEY,
The University of Illinois

Four years ago Professor Schneider published a volume of Lectures on Animal Psychology. The lectures were directed against mechanism in physiology and against the "nurphysiologische" psychologists. The writer argued for a panpsychic reservoir, for telic ideas, and for a psychic regulation of the organic functions (*cf. Psych. Bull.*, VII, 1910, 264). The reader who expects to make serious use of the speculations of the *Praktikum* should be familiar with the earlier work.

The plan of the present book is a discussion, dialogue-wise, by representatives from the different biological schools, of the problems of animal psychology and of general biology. A dramatic element is introduced into the dialogues by experimental demonstrations, and it is sustained by sharp repartee, clever thrust and riposte, and even personal censure and professional spite. A bit of characterization also is attempted. *Psychologe* is wise, judicial, impressive; *Biologe* is voluble and assured, but ultimately docile; while *Physiologe,* who represents *der Geist der stets verneint,* comes to his knees, in the end, confesses his sins, and swears allegiance to the rankest form of teleology. On one occasion, the Lamarckist (a vitalist, a monist and a Darwinian also figure in the discussions) accuses the physiologist of measuring the exactness of scientific research by the number of rabbits consumed in the laboratories. When he proposes to sacrifice, instead, a limited number of thoughts, the physiologist retorts: "Gedanken sind billiger als Kaninchen," to which the Lamarckist curtly rejoins: "Dann wundert's mich, dass man so wenig von Gedanken spürt."

The new work is *echt deutsch gedacht,* and the range of its discussion and of its knowledge is, moreover, limited, for the greater part, to German themes and to German studies. There

---

[1]*Veit*, Leipzig, 1912, pp. 719.

are three main subdivisions. In the first, discussion and experimentation center in the problems of perception, especially the necessity for a psychical factor in the integration of form. The second part treats of action. Here appear current views regarding the relative importance to organic movements of stimulus, receptor, centre, effector, impulse, telic ideas, will, and psychical energy. The physiologist, *e.g.*, holds to the efficacy of the simple homogeneous stimulus. The Darwinist proposes his *Psychoid*, the biologist his *Gegenwelt*, and the psychologist his "peripheral subject." The title of the third part, *Erfahrung*, refers to the author's theory of consciousness in the higher forms. Chapters are devoted to habit, memory, dreams, play, intelligence, and speech. The final synthesis is principally biological and philosophical speculation. Those who have followed the recent development of speculative biology in Germany will be entertained by the discussion of theories and by Professor Schneider's own constructions.

The comparative psychologist's chief interest in the book lies in the description and the discussion of the experiments. The volume will be useful as a reference book in the laboratory (the illustrations and the index are good), and it might serve—at least in this country—as a point of departure for study in the seminary.

2